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A New Genus and Two New Species of Unusual Dromiid Crabs (Brachyura: Dromiidae) from Northern Australia

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ABSTRACT. A new genus, *Desmodromia* n.gen., and two new species of dromiid crabs are described from northern Australia. In *Desmodromia* the rostrum is tridentate, the anterolateral teeth are well developed, the last two pairs of legs have no opposing propodal spines, and the dactyli on these limbs are rotated. The new genus is similar to *Epipedodromia* Andre, 1932 and *Homalodromia* Miers, 1884, but may differ from them in using bivalve shells for camouflage instead of sponges. *Desmodromia* shares some pereopod characters with the shell-carrying genus *Hypoconcha* Guérin-Meneville, 1854, but these characters probably evolved independently.

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McLay (1998) recently described a new genus and species of the Dromiidae from the Timor Sea, northern Australia. *Alainodromia timorensis* McLay, 1998 was described from collections made almost one hundred years ago by the Royal Navy but which laid unrecognised in the collections of the British Museum. Here I describe two new species, belonging to another new genus, collected from the same general area during the 1930's but until now overlooked amongst the extensive collections of the Australian Museum, Sydney. The existence of this new material was alluded to by McLay (1993: 225).

This paper is the first of a series of papers on the dromiid crabs of Australia. The generic revision of the family by McLay (1993) changed many of the names of the Australian

fauna and created several new genera for species already known. Besides *Desmodromia* n.gen., the list of Australian genera includes *Dromidiopsis* Borradaile, 1900, *Lauridromia* McLay, 1993, *Dromia* Weber, 1795, *Haledromia* McLay, 1993, *Fultodromia* McLay, 1993, *Paradromia* Balss, 1921, *Petalomera* Stimpson, 1858, *Stimdromia* McLay, 1993, *Conchoecetes* Stimpson, 1858, *Austrodromidia* McLay, 1993, *Cryptodromiopsis* Borradaile, 1903, *Cryptodromia* Stimpson, 1858, *Epigodromia* McLay, 1993, *Epipedodromia* Andre, 1932 and *Alainodromia* McLay, 1998.

Measurements given are carapace width × carapace length (CW×CL) in millimetres, and indicate the maximum dimensions.

Dromiidae De Haan, 1833

***Desmodromia* n.gen.**

Diagnosis. Carapace about as wide as long or slightly wider than long, subpentagonal, surface flattened or slightly convex, smooth or finely granulated. Rostrum tridentate, supraorbital margin and anterolateral teeth flattened and eave-like. Chelipeds about same size as first pair of walking legs and without epipod. Chelipeds and legs armed with long thin crest-like ridges. Female sternal sutures end apart between bases of first walking legs. Last two pairs of legs reduced, no propodal spines opposing dactyli. All abdominal segments freely movable. Uropods well developed, visible externally and used in abdominal locking mechanism.

Type species. *Desmodromia griffini* n.sp. by present designation.

Etymology. The generic name *Desmodromia* is a combination of Desmond, the first name of Des Griffin, and the generic name *Dromia*. The new generic name recognises the contribution of Des to the study of Australian brachyurans, in particular his work on the Majidae and Dromiidae.

Discussion. The discovery of *Desmodromia* n.gen. adds another genus to a group of similar dromiid genera which includes *Homalodromia* Miers, 1884, and *Epipedodromia* Andre, 1932. Prior to 1932, *E. thomsoni* Fulton & Grant, 1902 was known as *Platydromia thomsoni* Fulton & Grant, 1902. Apart from *Homalodromia*, which is widely distributed in the Indo-Pacific, both the other genera are endemic to Australian waters. *Homalodromia coppingeri* Miers, 1884 is known from New Caledonia but has not yet been reported from Australia (see McLay, 1993). *Homalodromia* and *Epipedodromia* are monotypic.

The characters shared by *Epipedodromia*, *Homalodromia* and *Desmodromia* are: no epipod on the cheliped, small size, carapace largely smooth, chelipeds small, about same size as first walking legs, last two pairs of legs reduced, last pair subdorsal. Differences between the three genera are summarised in Table 1. The most important differences between them are: the rostrum is tridentate in *Desmodromia* (bidentate in the other two), the anterolateral teeth are well developed in *Desmodromia* (absent or very small in the other two), the last two pairs of legs lack opposing propodal spines, the dactyli are rotated in *Desmodromia* (present and normal in the other two), and *Epipedodromia* lacks uropods (present in the other two and used in the abdominal locking mechanism).

Table 1. Comparison of *Epipedodromia* Andre, 1932, *Homalodromia* Miers, 1884, and *Desmodromia* n.gen.

	<i>Epipedodromia</i>	<i>Homalodromia</i>	<i>Desmodromia</i>
ratio CW/CL	as wide as long	width less than length	as wide or slightly wider than long
carapace surface	minutely granulate	smooth	smooth or finely granulated
rostrum	bidentate, eave-like	bidentate, teeth subacute, on prominent broad eaves	tridentate, eave-like
anterolateral margin	teeth absent	teeth very small	teeth well developed, eave-like
last two pairs of legs	third leg shortest, dactyl opposed by one propodal spine; fourth leg shorter than first leg, dactyl opposed by one propodal spine	third leg shortest, dactyl opposed by one propodal spine; fourth leg about as long as first leg, dactyl opposed by one propodal spine	both legs shorter than first leg, third shortest; no opposing propodal spines; dactyli rotated at right angle to limb axis
sternal sutures	end apart between chelipeds on raised ridge	end apart on tube-like structures behind chelipeds	end apart between bases of first walking legs
uropods	absent	small, visible externally, used in abdominal locking mechanism	small, visible externally, used in abdominal locking mechanism
depth	shallow waters to 60 m	24–50 m	shallow waters to 15 m
maximum CW	11–12 mm	11–12 mm	around 10 mm
camouflage	unknown, but probably sponge	sponge	?bivalve shells
distribution	southern Australia	Indo-West Pacific, but not known from Australia	northern Australia

Desmodromia griffini n.sp.

Figs. 1a–d, 3a

Material examined. HOLOTYPE Darwin Harbour (*sic* Port Darwin), Australia, dredged, 9.2 m, no date, 1 ♀, 9.5×9.1 mm (AM registration number: P10443) (coll. F. Reynolds Morris).

Description. Carapace wider than long, only slightly convex, almost flat, surface minutely granulate. Branchial and cardiac grooves only faintly evident. Frontal groove not evident but two low swellings present behind frontal area. Rostrum tridentate, median tooth, blunt, strongly deflexed, longer than lateral teeth but not visible dorsally. Lateral teeth rounded, directed anteriorly, continuing posteriorly as a slightly concave supraorbital shelf above eyes, ending at postorbital corner as a rounded lobe. Beneath this lobe there is a steeply descending concave margin to orbital fissure. Suborbital margin truncate. Anterolateral carapace margin begins at level of postorbital corner, armed with two teeth. First tooth broad, flattened, eave-like, anterior corner separated from postorbital corner by small gap. Second tooth blunt and set at higher level, follows closely behind first, its posterior margin continued without interruption to small blunt posterolateral tooth behind branchial groove. Posterolateral margins subparallel, bearing several small tubercles.

First article of antenna much wider than long, beaked medially, not gaping, upper lobe strongly down-curved. Second article longer than wide, surface convex, lateral margin near base bluntly produced, distomedial corner produced as blunt spine on which third article is inserted at an angle. Tip of exopod bilobed, reaching joint between third and fourth articles, inner lobe curving over base of eyestalk. Epistome smooth, concave.

Subhepatic area slightly convex, surface minutely granulate, beneath suborbital margin is small blunt tubercle, and raised area adorned by prominent crescent shaped ridge, with larger granules, enclosing several tubercles. Crista dentata has seven or eight blunt spines. Sternal sutures 7/8 terminate apart between bases of first walking legs on prominent circular tubercles.

Chelipeds lightly built, not much longer than first pair of walking legs, surface minutely granulated. Merus trigonal, surface smooth, corners produced and crest-like. Margins of carpus also crest-like, outer face carries two semi-continuous central ridges, and distal border is produced as two lobes. Outer face of propodus has central longitudinal crest, interrupted to produce small flanges; edges of upper propodal surface produced, making surface concave, left propodus carries longitudinal ridge and small proximal tubercle, while right propodus has ridge interrupted, forming two small swellings. Fingers almost straight, gaping, upper surface of dactyl bears longitudinal ridge, both fingers hollowed out internally and armed with 8–9 well-developed teeth.

Surfaces of first two pairs of walking legs minutely granulated, borders of all articles except dactyli produced, crest-like, inner margins of dactyli armed with five small spines increasing in size distally.

Last two pairs of legs reduced, last pair subdorsal, dactyli short, curved and without any opposing propodal spines.

All segments of female abdomen freely movable, surface smooth, borders produced, especially at posterolateral corners, uropods well developed and visible externally. Telson wider than long with convex posterior margin. Abdominal locking mechanism not functional (tubercles absent on coxae of first walking legs) because specimen is a mature female.

Etymology. The specific name uses the surname of Des Griffin.

Camouflage. Although the type specimen was not accompanied by a piece of camouflage, *D. griffini* may carry a bivalve shell for camouflage (see Discussion below).

Depth. The female was dredged from shallow water around 10 m.

Distribution. Known only from the type locality, Darwin Harbour, Australia.

Desmodromia tranterae n.sp.

Figs. 2a–d, 3b

Material examined. HOLOTYPE Ninety Mile Beach, between Broome and Wallal, Australia, dredged, 14.7 m, 1930: 1 ♀, 7.2×7.0 mm (AM registration number: P9910) (coll. Captain R. Bourne).

Description. Carapace about as wide as long, surface slightly convex, regions not defined, branchial groove not evident. Rostrum tridentate, median tooth well developed, strongly deflexed but visible dorsally. Lateral teeth combined with supraorbital margin that is greatly expanded over eyes. Margin of left supraorbital eave interrupted by two small notches, but on right hand side only single notch present. Posterior margin of supraorbital eave produced, almost meeting anterolateral tooth. Orbital fissure deep, suborbital margin unarmed, truncate. Anterolateral carapace margin begins at level of postorbital corner, armed with single, broad eave-like tooth whose exact shape differs on each side. Anterolateral tooth continued posteriorly and expands to form widest point of carapace. No posterolateral tooth, posterolateral margins convergent.

First article of antenna much wider than long, beaked medially, gape narrow, upper beak strongly down-curved. Second article much longer than wide, narrowing mid-way, surface convex, lateral margin near base bluntly produced, distomedial corner produced as blunt spine on which third article is inserted at an angle. Tip of exopod bilobed, reaching joint between third and fourth articles, inner lobe curving over base of eyestalk. Epistome smooth, concave.

Subhepatic area convex, surface minutely granulated, shaped to closely accommodate cheliped, small tubercle near suborbital margin and another near corner of third maxilliped. Crista dentata bearing six or seven small sharp spines. Female sternal sutures 7/8 end apart without

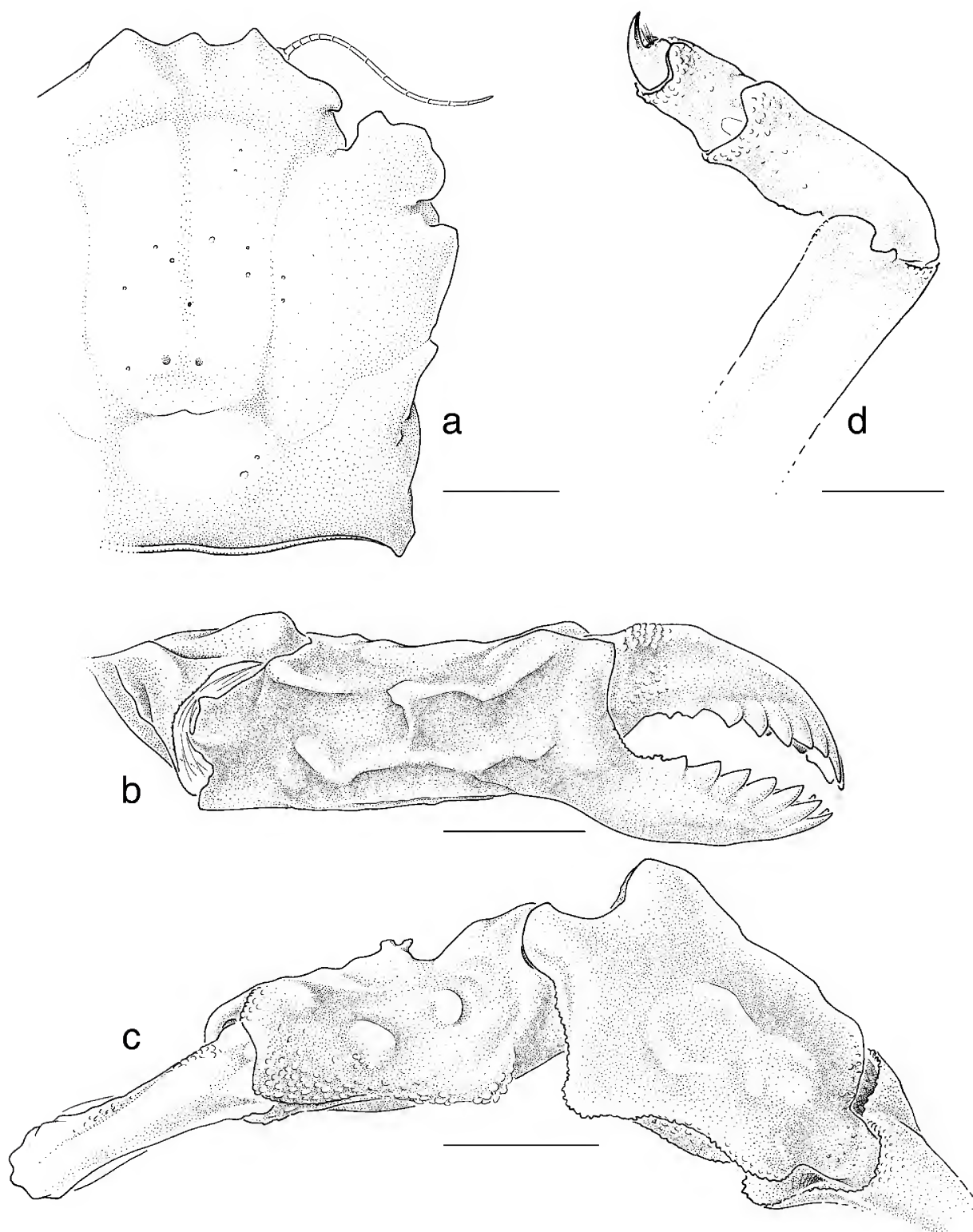


Figure 1. *Desmodromia griffini* n.sp., ♀, 9.2×9.1 mm, holotype, Port Darwin, Australia, 9.2 m: a, dorsal view of right half of carapace; b, outer face of right cheliped; c, dorsal view of right cheliped; d, dorsal view of left fourth leg (AM P10443). Scale bars represent 2 mm for a–c and 1 mm for d.

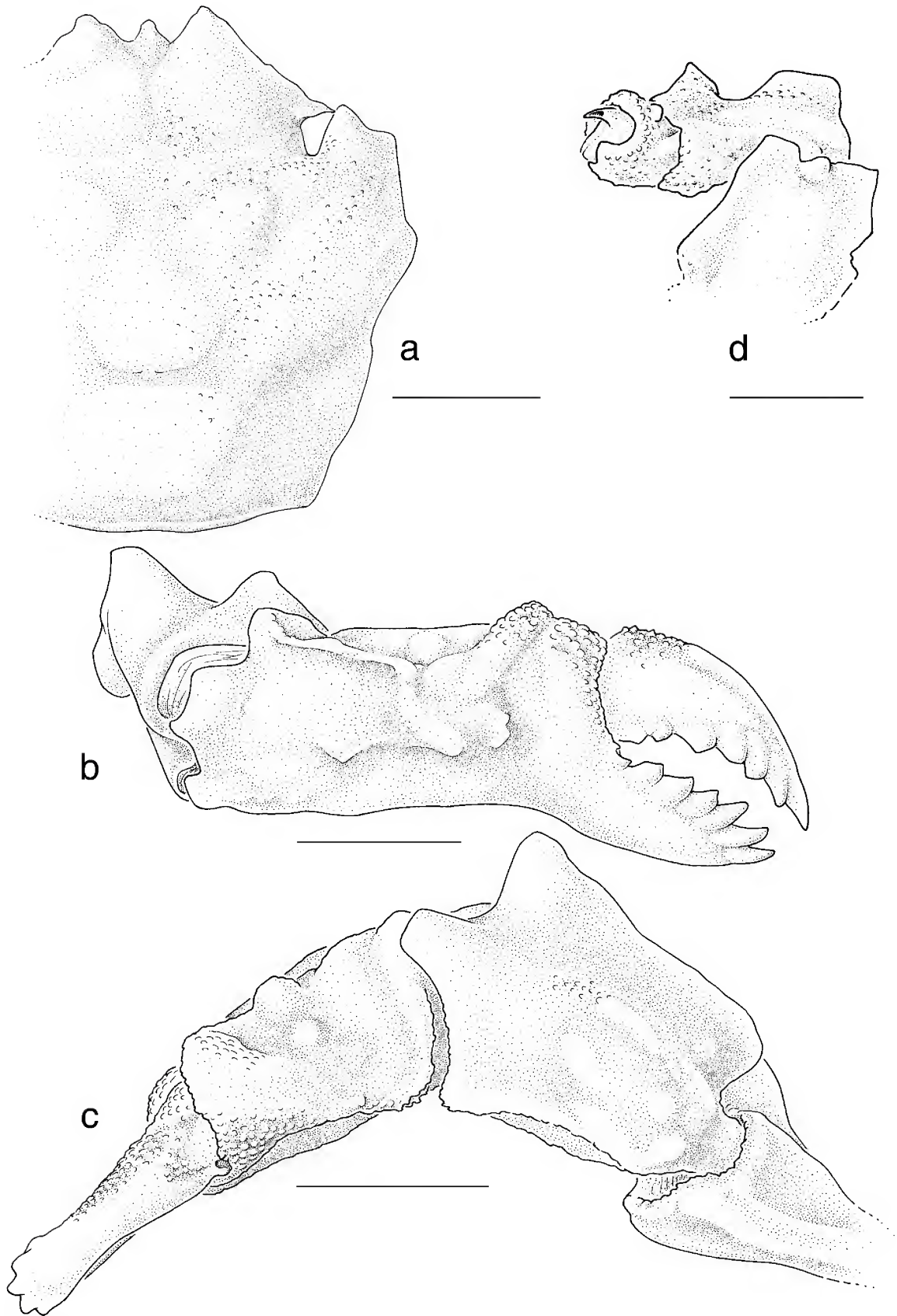


Figure 2. *Desmodromia tranterae* n.sp., ♀, 7.2×7.0 mm, holotype, Ninety Mile Beach, between Broome and Wallal, Australia, 14.7 m: a, dorsal view of right half of carapace; b, outer face of right cheliped; c, dorsal view of right cheliped; d, anterior view of left third leg (AM P9910). Scale bars represent 2 mm for a–c and 1 mm for d.

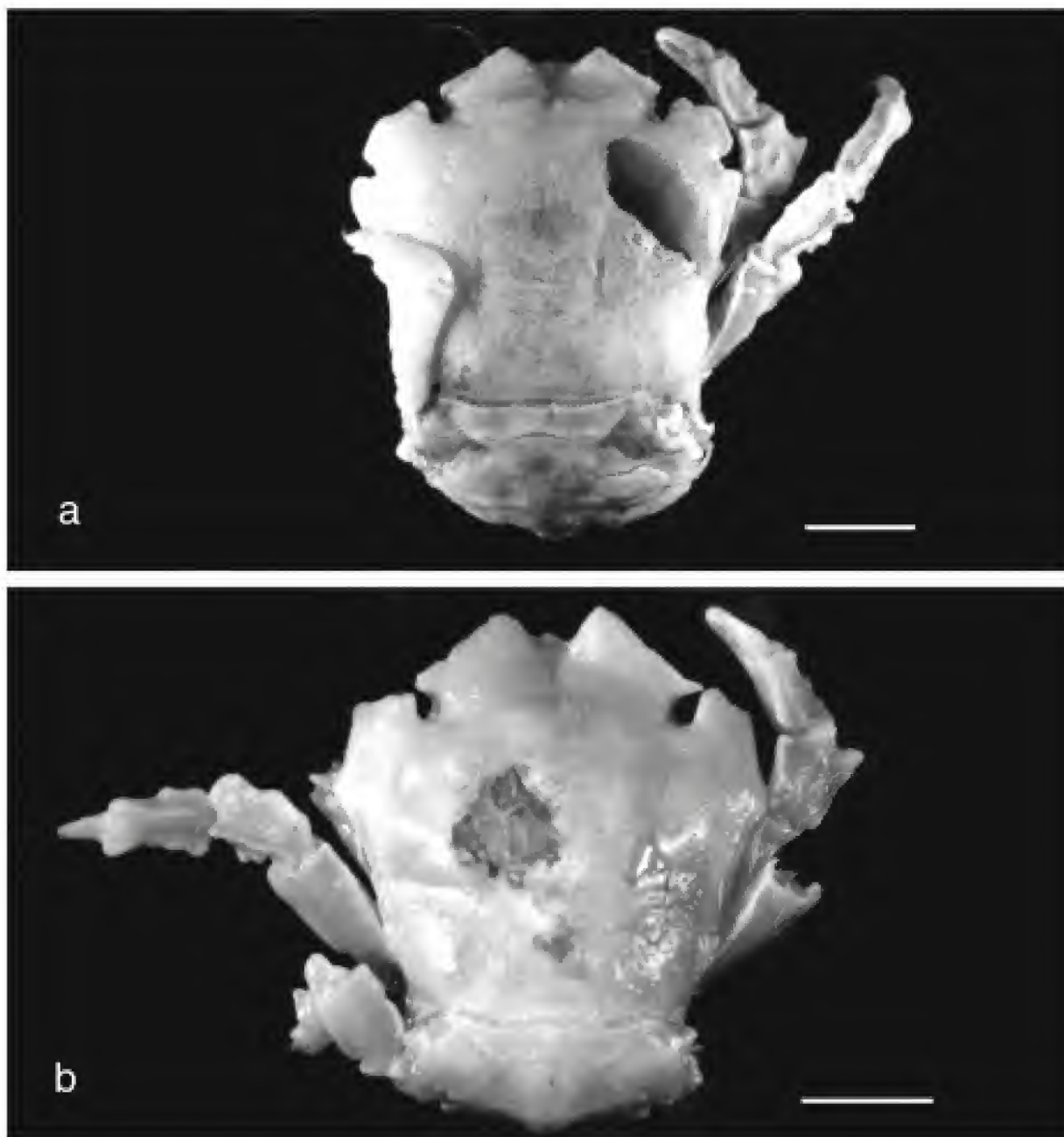


Figure 3. a, *Desmodromia griffini* n.sp., ♀ 9.2×9.1 mm, holotype, Darwin Harbour, Australia, 9.2 m (AM P10443): dorsal view of whole crab, left cheliped and first three legs, and the last three right legs not shown. Scale bar represents 3 mm. b, *Desmodromia tranterae* n.sp., ♀ 7.2×7.0 mm, holotype, Ninety Mile Beach, between Broome and Wallal, Australia, 14.7 m (AM P9910): dorsal view of whole crab, left second and fourth legs, and part of the first, and last three right legs not shown. Scale bar represents 2 mm. In both photos the darker area on each carapace indicates accidental damage incurred after the drawings were made.

tubercles between bases of second walking legs. The type specimen is an immature female, so the sternal sutures may have not reached their full length, as found in *D. griffini* (see above).

Chelipeds small, margins of articles produced and crest-like. Upper surface of carpus concave, distal margin produced as two lobes. Outer face of propodus with

longitudinal ridge bearing two flanges and joined to margin above it; upper surface concave with two small rounded tubercles on right propodus, but these are absent on left hand side. Fingers straight, upper margin of dactylus crest-like, margins armed with six or seven well-developed teeth.

Articles of first two pairs of walking legs have crest-like

margins, inner margins of dactyli armed with five or six small spines.

Last two pairs of legs reduced, last pair subdorsal, dactyli short, curved and without any opposing propodal spines.

Abdominal segments freely movable, surface smooth, borders produced, especially at posterolateral corners, segments five and six have pair of blunt medial tubercles on raised ridge, separated from lateral margins by deep channels that continue on to telson. Uropods well developed and visible externally, fitting in front of small tubercles on coxae of first walking legs. The type is an immature female so abdominal locking mechanism still functions. Telson wider than long, posterior margin truncate.

Etymology. The specific name for this new species acknowledges the contribution of Mrs Helen Tranter, the long-serving research assistant of Des Griffin, to the study of Australian decapods.

Camouflage. No camouflage material was included with the *D. tranterae* specimen. This species may carry bivalve shells for camouflage (see Discussion below).

Depth. Only known from shallow water of around 15 m.

Distribution. *Desmodromia tranterae* is only known from North Western Australia.

Key

The following key may be used to separate the species of *Epipedodromia*, *Homalodromia* and *Desmodromia* discussed in this paper.

- 1 rostrum tridentate, anterolateral teeth well developed, eave-like 2
- rostrum bidentate, anterolateral teeth absent or very small and concealed beneath margin 3
- 2 two notches in anterolateral margin, clearly defining two eave-like teeth *Desmodromia griffini* n.sp.
- only a single notch in anterolateral margin defining one broad eave-like tooth *Desmodromia tranterae* n.sp.
- 3 behind frontal carapace margin is a prominent arcuate ridge divided into four equal parts by deep grooves, uropods absent *Epipedodromia thomsoni* (Fulton & Grant, 1902)
- arcuate ridge on carapace absent, uropods present *Homalodromia coppingeri* Miers, 1884

Discussion

The structure of the last two pairs of legs of both the new species suggests that they may use a different kind of camouflage material from most other dromiids. The dactyli on both limbs are small, stout, and curved and not opposed by propodal spines. In most dromiids, these propodal spines form a subchelate mechanism used for grasping pieces of soft camouflage material like sponges or ascidians. The third pair of legs hold the posterior margin while the longer fourth pair hold the anterior margin of the camouflage cap. While the relative size of the two limbs is similar to other dromiids, *D. griffini* and *D. tranterae* lack a subchelate mechanism.

In sponge-carrying crabs (e.g., species of *Dromidiopsis* and *Cryptodromia*), the dactyli are long and thorn-like, opposed by one or more propodal spines, and their axis is the same as that of the preceding articles. In both of the new species, however, the dactyli of the last two pairs of

legs are rotated through 90° and are therefore directed at right angles to the axis of the rest of the limb. These species may not carry soft camouflage material, but instead use something hard like bivalve shells.

The structure and orientation of the dactyli of the last two pairs of legs is similar to that found in the genus *Hypoconcha* Guérin-Meneville, 1854 whose species are known to carry bivalve shells. The third pair of legs fit into the bivalve hinge line, while the fourth pair grasp the edges of the shell. Besides the structure of the last two pairs of legs, the species of *Desmodromia* also share other similarities with *Hypoconcha*: presence of strong eaves overhanging and protecting the eyes and a flattened carapace surface that would allow the crab to fit closely under the shell. Also the carapace is poorly calcified, although not membranous as is found on the posterior half of the carapace in *Hypoconcha*. All of these shared characters point to *Desmodromia* being another shell-carrying dromiid genus.

Besides *Hypoconcha*, which is found around tropical American coasts, the only other shell-carrying genus is *Conchoecetes* Stimpson, 1858, which has a wide distribution in the Indo-West Pacific, including Australia. However, the method of grasping the shell is different in *Conchoecetes*. Members of this genus use large talon-like dactyli on the third legs to grasp the hinge line of its bivalve shell while the fourth legs are reduced and not so important for shell carrying. Also *Conchoecetes* has an epipod on the cheliped whereas *Hypoconcha* does not. For these reasons, *Desmodromia* is more like *Hypoconcha* than *Conchoecetes*.

However, the similarity of *Desmodromia* to *Hypoconcha* only relates to the structure of the last two pairs of legs and I think that it represents a case of parallel evolution. *Hypoconcha* has several characters (e.g., the absence of a rostrum, the peculiar lunate coxae of the pereopods) not necessarily related to camouflage, which make them a separate group. McLay (1993) indicated that the species of *Hypoconcha* should be placed in a separate family. Recently, McLay *et al.* (in press) compared the larval characters of *Hypoconcha* and *Conchoecetes* with other dromiids and the new family should include both these genera. This information suggests that the two best-known shell carrying genera shared a common ancestor. Meanwhile *Desmodromia* has many dromiid characters that suggest they belong amongst the Dromiidae. Thus, I propose that shell carrying evolved twice, once in the ancestor of *Hypoconcha* and *Conchoecetes*, and once in the group to which *Desmodromia* belongs (see Table 1).

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Equisetalean Plant Remains from the Early to Middle Triassic of New South Wales, Australia

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ABSTRACT. Equisetalean fossil plant remains of Early to Middle Triassic age from New South Wales are described. Robust and persistent nodal diaphragms composed of three zones; a broad central pith disc, a vascular cylinder and a cortical region surrounded by a sheath of conjoined leaf bases, are placed in *Nododendron benolongensis* n.sp. The new genus *Townroviarnites* is erected for stems previously assigned to *Phyllothea brookvalensis* which bear whorls of leaves forming a narrow basal sheath and the number of leaves matches the number of vascular bundles. Finely striated stems bearing leaf whorls consisting of several foliar lobes each formed from four to seven linear conjoined leaves are described as *Paraschizoneura jonesii* n.sp. Doubts are raised about the presence of the common Permian Gondwanan sphenophyte species *Phyllothea australis* and the Northern Hemisphere genus *Neocalamites* in Middle Triassic floras of Gondwana.

HOLMES, W.B. KEITH, 2001. Equisetalean plant remains from the Early to Middle Triassic of New South Wales, Australia. *Records of the Australian Museum* 53(1): 9–20.

The plant Phylum Sphenophyta, which includes the equisetaleans, commonly known as “horse-tails” or “scouring rushes”, first appeared during the Devonian Period (Taylor & Taylor, 1993). By the Carboniferous Period the Sphenophyta had reached their greatest degree of diversity, when, as semi-aquatic or swamp-dwelling scramblers, small herbaceous plants or even trees to 20 m in height, they formed a prominent part of the vegetation of the coal swamps of northern Pangaea, or, what is today, Europe and North America (Boureau, 1964). During the

Permian Period, the increasing aridity and decline in the vegetation of northern Pangaea was in contrast to that in southern Pangaea—Gondwana—where flourishing swamp forests of the *Glossopteris* Flora were producing some of the world’s greatest coal reserves. A limited range of sphenophytes (Townrow, 1955; Rigby, 1966; McLoughlin, 1992a,b; Holmes, 1995) including *Phyllothea australis*, a significant contributor to the formation of the coal (Beeston, 1991; McLoughlin, 1993) and fodder for dicynodont mammal-like reptiles (Rayner, 1992), were associated with *Glossopteris*.

The catastrophic end-Permian extinction event brought about the demise of the *Glossopteris* Flora (Retallack, 1995; McLoughlin *et al.*, 1997). A new, low diversity flora appeared in the Early Triassic sediments overlying the topmost Permian coal seams in the Sydney Basin. This flora included the pteridosperm "*Thinnfeldia*" *callipteroides*, some ferns, conifers and lycopods, the sphenophyte *Schizoneura gondwanensis* and other associated equisetalean remains (Retallack, 1980). By the late Middle Triassic, the vegetation of Gondwana had diversified to a degree that was not surpassed until the rise to dominance of the angiosperms in the Cenozoic (Anderson *et al.*, 1999). During the Middle and Late Triassic, equisetalean sphenophytes had a cosmopolitan distribution and often formed monoculture thickets in waterlogged environments. However, they failed to regain the diversity reached during the Carboniferous Period.

From the Early and Middle Triassic of New South Wales, fossil equisetaleans of varying degrees of preservation are known from the Sydney Basin (Walkom, 1925; Townrow, 1955; Retallack, 1973, 1980), the Lorne Basin (Holmes & Ash, 1979), the Great Artesian Basin (Holmes, 1982) and the Nymboida Coal Measures (Retallack, 1977; Holmes, 2000; see Fig. 1). Subsequent to the Triassic, the sphenophytes went into a decline and today they are represented by a single genus, *Equisetum* with about 20 extant species (Hauke, 1983; Taylor & Taylor, 1993) none of which occur in Australia.

With the exception of a silicified stem *Spaciinodum collinsonii* Osborn & Taylor, 1989, from Antarctica and a nodal diaphragm *Nododendron suberosum* Artabe & Zamuner, 1991, from Argentina, Gondwana Triassic equisetaleans are poorly documented and illustrated. In some cases, leaf-bearing stems have been referred, on doubtful grounds, to species described from the Northern Hemisphere or from different geological periods.

The Palaeontology Collection of the Australian Museum includes some noteworthy Triassic equisetalean material that is here described and illustrated.

Systematic palaeobotany

Phylum Sphenophyta

Order Equisetales incertae sedis

Genus *Nododendron* Artabe & Zamuner, 1991

Type species. *Nododendron suberosum* Artabe & Zamuner, 1991—nodal diaphragm only, Potrerillos Formation, Cacheuta Basin, Argentina. Early Late Triassic.

Emended diagnosis. Equisetalean nodal diaphragms differentiated into three zones; a central medullary disc of robust persistent tissue encircled by a vascular cylinder composed of a ring of vascular bundles two or more times more numerous than number of leaves in surrounding whorl; and a cortex composed of inner ring of periderm and outer ring of secondary growth in the cortex and/or sheath of conjoined and persistent leaf bases.

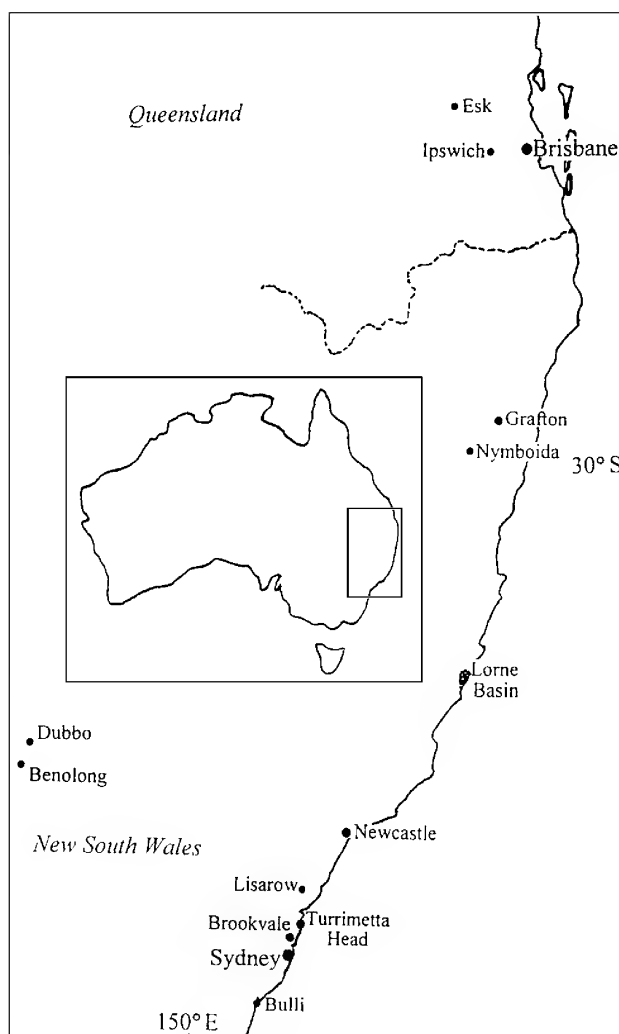


Figure 1. Eastern Australian fossil equisetalean localities mentioned in text.

Nododendron benolongensis n.sp.

Figs. 2A–C, 3A–C

Diagnosis. A diaphragm with ring of closely spaced vascular bundles; cortical zone undulate with fluted margins, surrounded by persistent sheath of conjoined leaf bases. Vascular bundles twice number of leaves.

Description. Eight almost complete nodal diaphragms together with fragments of equisetalean stems and ginkgoalean leaves are preserved as impressions on the surface of the partially baked claystone slab AM F51397 (Fig. 2A).

The nodal diaphragm selected as the holotype, (Fig. 2B) is preserved as a slightly distorted disc with an external diameter of 18 to 23 mm. The medullary disc has a smooth surface and a diameter of 9 to 12 mm. Surrounding the pith disc is a vascular cylinder with a ring of c. 48 bundles, each circular to triangular in cross section. A cortical zone, c. 3 mm in width, surrounds the vascular cylinder. The outer portion of the cortex is undulate or fluted and surrounded

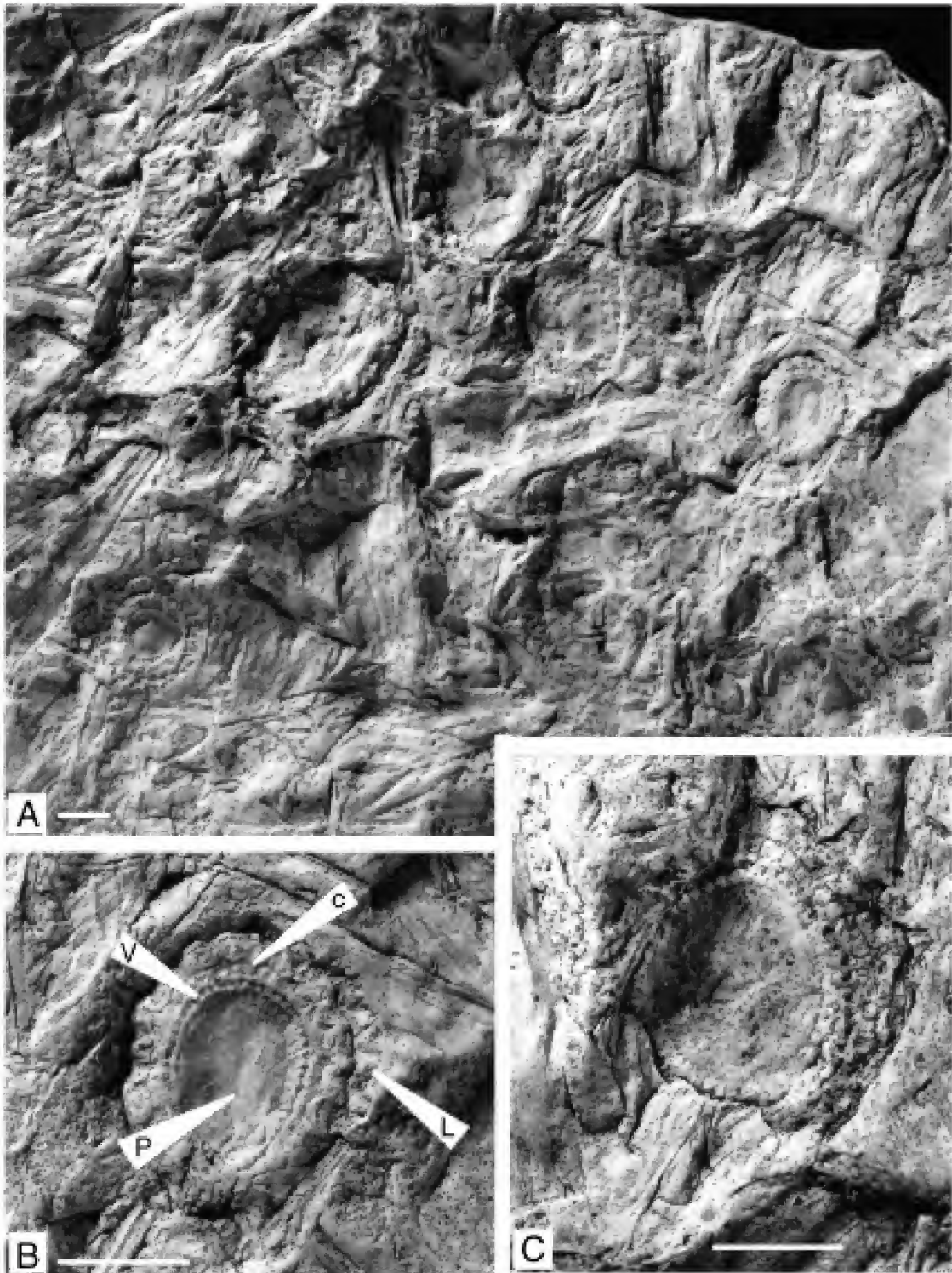


Figure 2. A–C, *Nododendron benolongensis* n.sp. from Benolong. A, AM F51397, portion of a large slab with eight nodal diaphragms, fragments of sphenophyte leaves and stems and portions of *Sphenobaiera ugotheriensis* leaves. B, holotype, AM F113364; P, pith or medullary zone; V, vascular cylinder with ring of vascular bundles; c, cortical zone; L, leaf lamina contracting from basal sheath. C, paratype, AM F113374. Scale bars 1 cm.

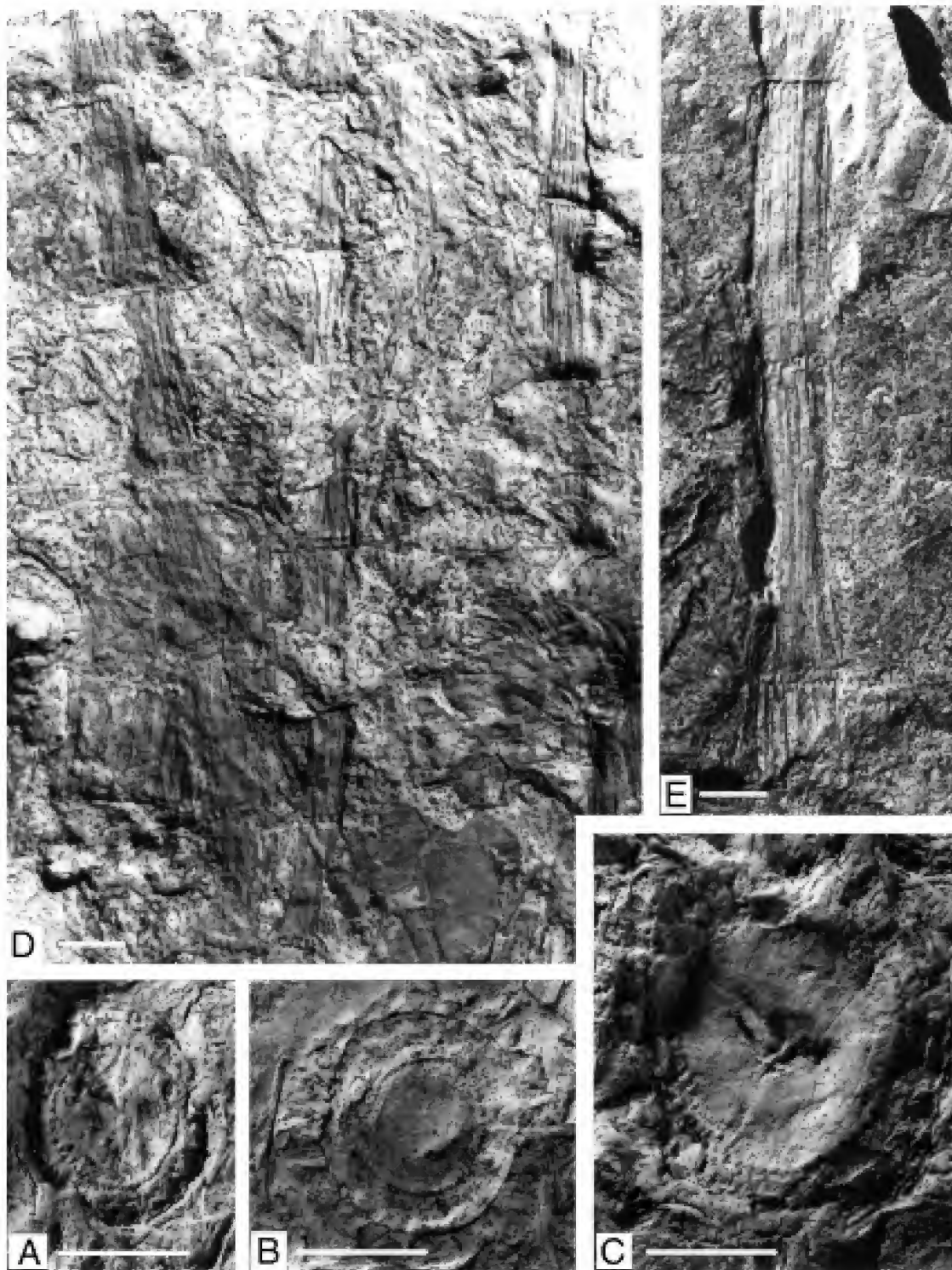


Figure 3. A–C, paratypes, *Nododendron benolongensis* n.sp. from Benolong. A, AM F113373; B, AM F113363; C, AM F113365. D,E, equisetalean stems associated with *Nododendron benolongensis* from Benolong; D, AM F61114; E, AM F61113. Scale bars 1 cm.

by a sheath of conjoined leaf bases. The leaves contract and separate distally into linear laminae c. 1 to 1.5 mm wide. All the leaves are broken off close to the base so that their length is not known. Other nodal diaphragms on the slab are circular, from 18 to 30 mm in diameter and with rings of from 35 to 60 vascular bundles. There are half as many leaves as vascular bundles. Cell structure is not preserved on any of the diaphragms.

Type material. HOLOTYPE: AM F113364 Australian Museum, Sydney, New South Wales. PARATYPES: AM F113362, F113363, F113365 and F113366. All on slab AM F51397.

Type locality. “Ugothery”, Portion 31, Parish of Benolong, Dubbo, N.S.W. Napperby Formation, Great Artesian Basin, late Early to early Middle Triassic (see Holmes, 1982; Cameron *et al.*, 1999). Grid reference, 654600 6408900, Dubbo Geological Series Sheet, 1:250 000, 1999, 32°26'46"S 148°38'40"E.

Etymology: *benolongensis*—from the Benolong district, near Dubbo, New South Wales.

Discussion. *Nododendron suberosum* Artabe & Zamuner, the type species for the genus, is based on a single specimen (Number 2076B) and its counterpart (20167) which I have examined in the Palaeobotanical Collection of the Museo de La Plata, La Plata, Argentina. The specimen comprises a nodal diaphragm in transverse section and a dissociated portion of a longitudinal section of an equisetalean stem showing four nodes and three internodes all preserved as impressions with some limonite replacement of the original organic material. The surface of the specimen appears to have been treated with a surface hardener and the matrix between the node and the stem has been polished. Frenguelli (1949) first described the specimen and placed it in *Neocalamites carrerei* (Zeiller) Halle, originally erected for equisetalean foliage-bearing stems from the Upper Triassic of China (Zeiller, 1903). Based on an anatomical and morphological study, Artabe & Zamuner (1991) reassigned Frenguelli's specimen to *Nododendron suberosum*, including both the diaphragm and stem under the same name. Using a binocular microscope and low angle lighting I was unable to confirm the cell structure on the surface of the diaphragm as described by Artabe & Zamuner. The outer portion of the diaphragm illustrated on plate 2.2 of Artabe & Zamuner (1991) was described as a “branch with a whorl of *Asterophyllites*-type leaves”. My examination of this “whorl” showed it to be a fragment of a broad leaf with a number of irregular and discontinuous veins, preserved on the surface of a thin layer of sediment overlying and quite separate from the layer on which the *Nododendron* node is preserved. There was no evidence of nodes or whorls of leaves on any of the other “branches”, which I interpret as leaves.

The erection of *Nododendron* as a form genus for robust and detached equisetalean diaphragms is a useful means of classifying these plant organs that are commonly found dispersed and separate from the parent plant. I have emended the generic diagnosis to include nodal diaphragms only and, recognizing that the vast majority of fossil material will

not have cell structure preserved, the diagnosis is based only on gross morphological features.

Nododendron benolongensis differs from *N. suberosum* by the presence of a conspicuous ring of vascular bundles in the vascular cylinder; by the undulate and fluted appearance of the cortical zone; by the lack of visible vascular traces traversing the cortex and by its much smaller size. *Nododendron suberosum* appears to have about four times the more vascular bundles than leaves, compared with two bundles per leaf in *N. benolongensis*.

The single diaphragm assigned to ?*Nododendron* sp. from early Middle Triassic Nymboida Coal Measures of northern New South Wales (Holmes, 2000) is not sufficiently well preserved for specific identification.

A nodal diaphragm from the Ipswich Coal Measures of Queensland, illustrated by Hill *et al.* (1965, pl. T1, fig. 2) as *Neocalamites* cf. *carrerei* differs from *N. benolongensis* by the obscure vascular zone and by the wide cortical zone of rectangular or slightly wedge-shaped segments with a plicated appearance.

Other Gondwanan Triassic nodal diaphragms that differ in form from *Nododendron* and are closer to extant *Equisetum*, have been referred to *Equisetites* by Walkom (1915), Du Toit (1927) and Artabe (1985). Walkom (1925) assigned a node from the Narrabeen Series to *Phyllothea australis*. Gould (1968) noted that solid diaphragms are characteristic of *Equisetum* rather than *Phyllothea*. Persistent nodal diaphragms are notably absent from Permian *Phyllothea australis* assemblages (Townrow, 1955: 59) and I suspect that *Phyllothea australis* together with *Glossopteris* did not survive the end-Permian extinction event.

A nodal diaphragm from Argentina assigned to *Equisetites fertilis* (Artabe, 1985, pl. 1, fig. 2) appears to be divided into three zones as in *Nododendron*, but the preservation does not allow for a close comparison. In a revision of Kurtz (1921), Archangelsky *et al.* (1995) suggested that *E. fertilis* was an immature stage of *Neocalamites carrerei*. However, the presence of the persistent nodal diaphragms raises doubts that this plant is *N. carrerei* sensu Halle (1908).

Many Gondwanan equisetalean leaf-bearing stems have been placed in the genus *Neocalamites* (Halle, 1908), the diagnostic feature being that the leaves are free to the base. Complex and persistent nodal diaphragms have not been recorded in association with *Neocalamites* from the Northern Hemisphere. On both the Argentinian and Australian *Nododendron* nodes, the attached whorls of foliage, although very incomplete, show the leaves expanding and conjoining basally to form a continuous sheath around the node. I have examined the specimens of foliage-bearing stems from eastern Australia that were described as having leaves free to the base and were placed subsequently in either *Neocalamites hoerensis* or *N. carrerei* by Walkom (1915, pl. 2, fig. 1); Jones & de Jersey (1947, text-fig. 2); Hill *et al.* (1965, pl. T1, figs. 1,2) and Playford *et al.* (1982, pl. 2, fig. 7). In all cases, the material is not preserved well enough to determine the method of attachment of the leaf whorls to the node or whether the leaves were indeed free to the base. The presence of nodal

diaphragms and leaves conjoining to form a short basal sheath, as in *Nododendron* species from New South Wales and Argentina, suggests that some at least of Gondwana equisetaleans are generically distinct from the contemporaneous equisetalean plants from the Northern Hemisphere.

**Equisetalean stems associated with
*Nododendron benolongensis***

Figs. 3D,E

Closely associated with the nodal diaphragms described above, are numerous impressions of external moulds of equisetalean stems and fragments of detached linear leaves (Fig. 3D). None of the stems are preserved in a manner to show the attachment of the leaves. The external surface of the internodes is smooth, or coarsely and irregularly grooved, with the number of broad ribs approximating the number of leaf scars on the nodes. The nodes are slightly expanded and sometimes marked by a distinct transverse groove below the line of scars. Stems preserved as internal pith casts (Fig. 3E) show fine longitudinal striations representing the vascular bundles which are twice the number of the scars visible on the nodes. The width of the stems varies from 5 to 30 mm. The internodal length is roughly related to the width of the stem and position on the plant. Internodes are c. 50 mm long near the stem base but gradually decrease in length distally. On the nodes of compressed stems 12 mm wide, there are ten leaf scars visible, which indicates a complete whorl of 20 leaves. The ratio of vascular bundles to number of leaves is similar to that of *N. benolongensis* and *Neocalamites* (Halle, 1908) but differs from *Townroviarnites* n.gen. described below, which has the same number of leaves as vascular bundles.

Zalessky (1932) erected the form genus *Paracalamites* to include leafless stems on which the ribs and grooves passed through the nodes without alternation. A number of species have been erected for stems from the Permian of Siberia (Boureau, 1964) and from Australia (Rigby, 1966). As *Paracalamites*, by definition, is based on only a few characters, such as density of the ribs and ratio of stem width to internode length, which vary considerably between stems in the same assemblage, I believe that erecting a new species of *Paracalamites* for the Benolong stems would be of little value.

Although the stems illustrated in Fig. 3D,E have a smaller diameter than the nodal diaphragms illustrated in Figs. 2A–C, 3A–C, their close taphonomic association with *N. benolongensis* suggests they are probable biological associates.

Genus *Townroviarnites* n.gen.

Type species. *Townroviarnites brookvalensis* (Townrow, 1955: 53) **n.comb.** (from *Phyllothea*)

Generic diagnosis. Sphenophyte with longitudinal ribs passing without alternation through node. Nodal region complex, with a transverse groove bounded above and below by transverse ridges. Linear leaves conjoined close to base to form narrow collar at node. Number of leaves in

whorl the same as the number of vascular bundles in the internodal vascular cylinder.

Etymology. *Townrovia*—for Dr J.A. Townrow, eminent palaeobotanist who made significant contributions to the knowledge of Australian Triassic floras and who was the first to recognize this plant as a new taxon; *mites* suggests affinities with other equisetalean plants.

***Townroviarnites brookvalensis*
(Townrow, 1955: 53) n.comb.**

Figs. 4A–C, 5A–C

1955 *Phyllothea brookvalensis* Townrow, p. 53, text-figs. 4A–C, 5A,B.

The diagnosis for *Phyllothea brookvalensis* (Townrow, 1955: 53–54) was a lengthy and detailed description of the type material in the British Museum. That diagnosis is here emended to include the range of variation within all populations referable to this species.

Emended diagnosis. Stems with broad longitudinal ribs; nodes somewhat expanded, showing a transverse depression bounded by narrow transverse ridges. Leaves equal in number to vascular bundles. Leaves coalescing to form a short basal collar; linear, thick texture; median vein sometimes present; number of leaves in each whorl approximately equal to circumference of stem in millimetres.

Description. The type material of Townrow (1955) was based on a part of the Tillyard Collection from the Beacon Hill Quarry in the northern Sydney suburb of Brookvale and is housed in the Geology Department of the Natural History Museum, London. Additional material in the Australian Museum from the type locality and from a new locality at Lisarow near Gosford, extends our knowledge of the range of variation within this taxon.

From the Brookvale locality, one specimen (Fig. 4A) has two whorls of about 16 leaves to 65 mm long and to 1.5 mm wide. Another (Fig. 4C) has a single smaller whorl of c. 10 leaves, each to c. 20 mm long and to 1 mm wide.

The specimens from a now abandoned roadfill quarry in a white siltstone lens in the Terrigal Formation at Lisarow, near Gosford, consist of internal casts and external moulds of stems, a nodal diaphragm and whorls of leaves. An almost complete detached whorl of 30 leaves (Fig. 5A) borne around a stem 10 mm in diameter shows the leaves conjoining basally and decurving through 180° to form a vertical collar into the matrix. The leaves of the type material were stated by Townrow (1955) as having a “midrib clearly marked over most of the leaf”. In this additional material, the leaf midvein is rarely evident and the leaf lamina is often marked by several faint longitudinal striations, but this may be a feature of preservation due to wrinkling of the leaves along aligned epidermal cells. The nodal diaphragm (Fig. 5C), associated with 22 mm wide internal casts of finely striated stems (Fig. 5D), is preserved as a faint iron-stained impression with a vascular ring containing

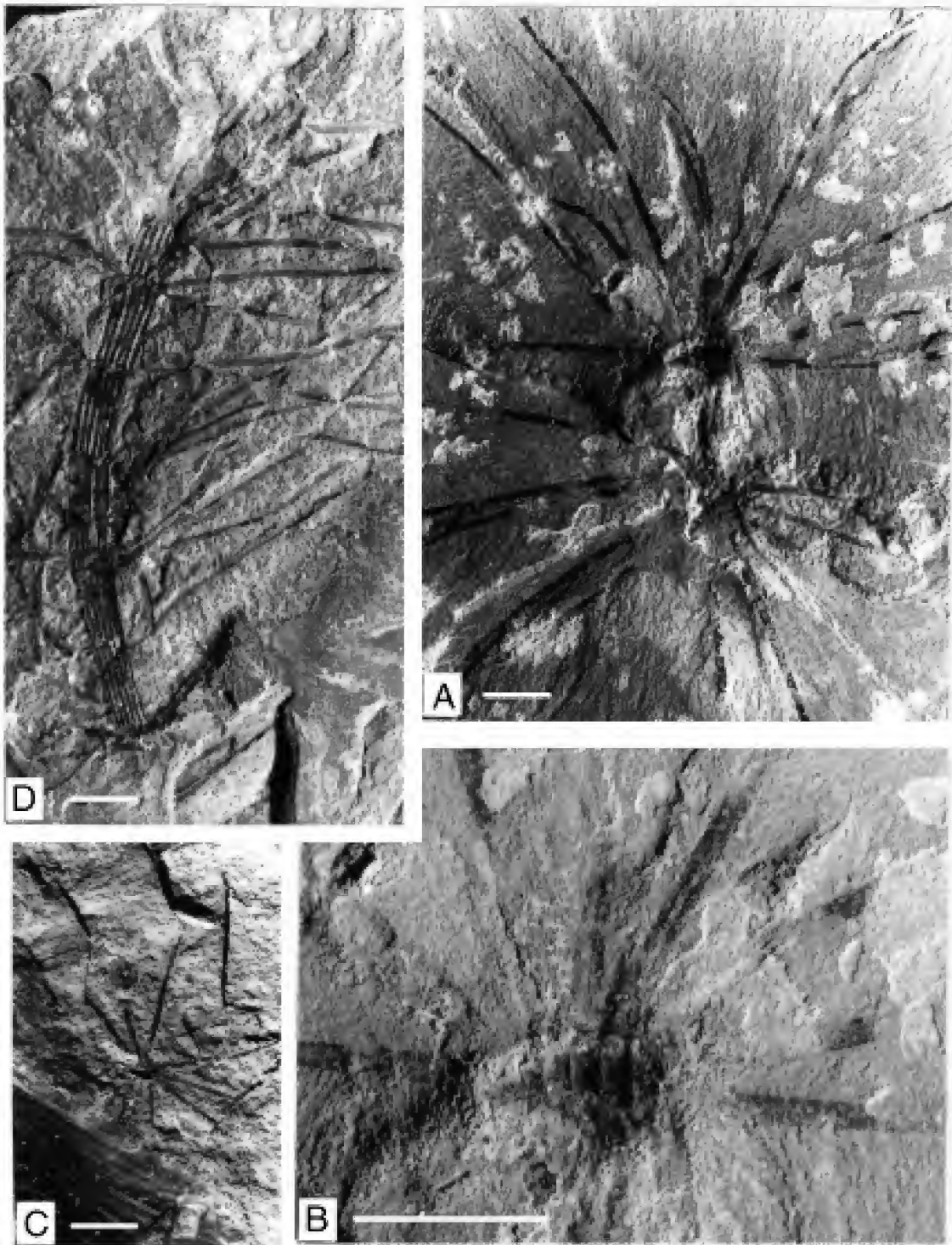


Figure 4. A–C, *Townroviarnites brookvalensis* n.comb. from Beacon Hill Quarry, Brookvale; A, AM F18616, two leaf whorls; B, AM F18616, portion of leaf whorl and node; C, AM F18617, small leaf whorl. D, AM F38273, equisetalean stem with apparently attached leaves associated with *T. brookvalensis*. Scale bars 1 cm.

c. 90 bundles in a stem with an external circumference of c. 94 mm. Preserved on the same horizon is an external mould of a stem (Fig. 5E) c. 10 mm wide and with internodes c. 30 mm long. Poorly defined external longitudinal ribs appear to pass without alternation across the nodes. There

is a transverse line of small circular leaf scars at each node, but the diagnostic transverse groove and ridges at the nodes are not evident.

Based on all available specimens of *T. brookvalensis*, the ratio of the number of leaves to stem circumference in

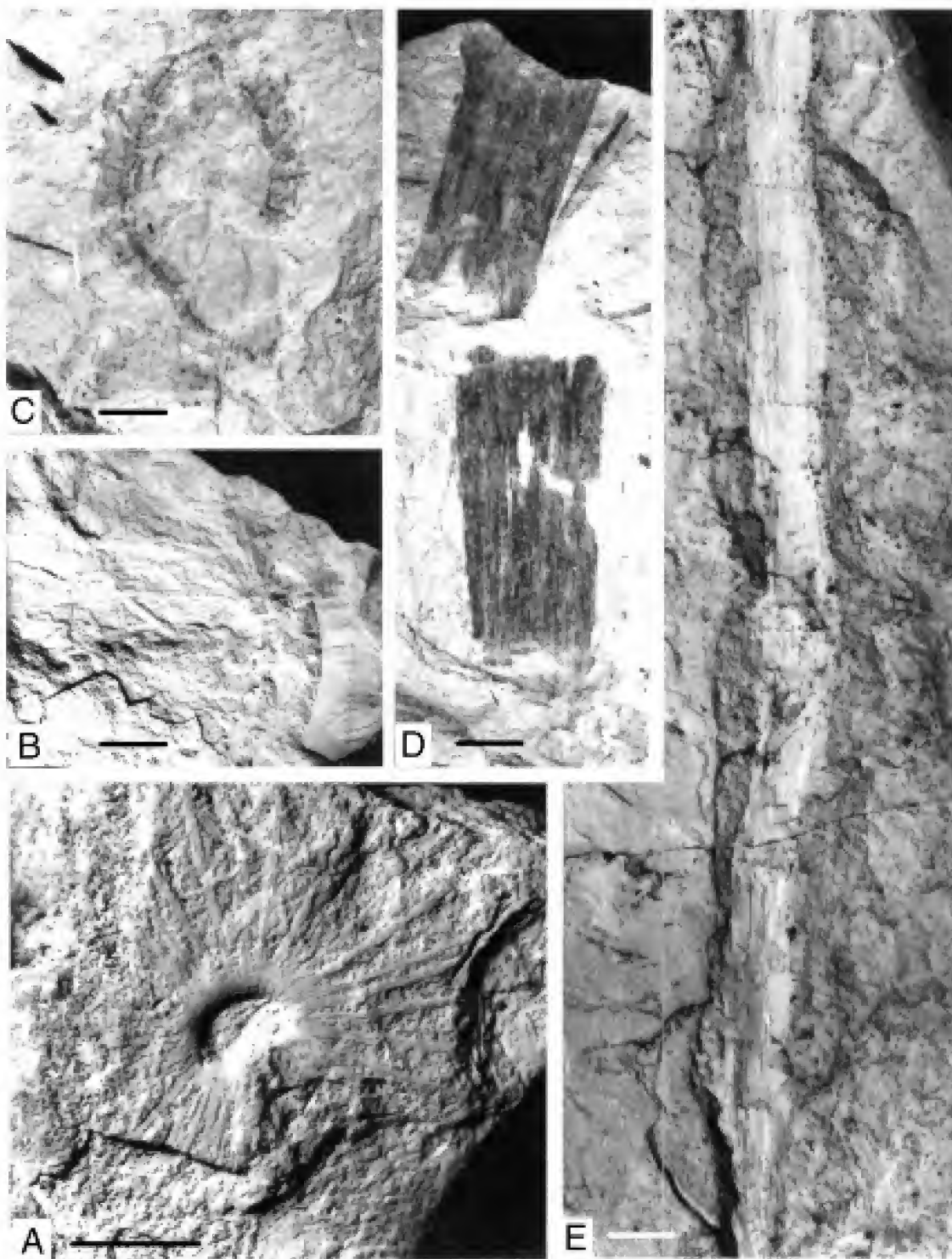


Figure 5. A–E, *Townroviamites brookvalensis* n.comb. from Lisarow Quarry; A,B, leaf whorls; A, AM F113356; B, AM F113358; C, nodal diaphragm with ring of vascular bundles, AM F113354; D, internal cast of large stem, AM F113354; E, external mould of stem with c. 10 leaf scars across nodes, AM F113359. Scale bars 1 cm.

mm ranges from 1:0.5 to 1:1.3 with an average of 1:1. This compares with a ratio of 1:4.5 and 1:2 for *Nododendron suberosum* and *N. benolongensis* respectively.

Type material. LECTOTYPE: V31862a, Natural History Museum, London. PARATYPES: V31857, V31859, V31860 (NHM).

Type locality. Beacon Hill Quarry, Brookvale, near Sydney. Brookvale Shale Lens of the Hawkesbury Sandstone, Sydney Basin, early Middle Triassic (Retallack, 1977, microfiche frame G10). GR 387 638, 1:100 000, Sydney Geological Series Sheet, 1983; 33°45'12"S 151°15'30"E.

Additional material. AM F18616, F18617 from Brookvale and AM F113352–61 from the Lisarow Quarry, Terrigal Formation, Sydney Basin; late Early to early Middle Triassic.

Discussion. In his original description of *Phyllothea brookvalensis*, Townrow (1955) expressed doubt as to the correct generic position of this equisetalean plant fossil, but he considered it nearest to *Phyllothea* and *Neocalamites*. *Townroviarnites* differs from *Phyllothea*, which is essentially a Permian genus (see above), by its reduced leaf sheath and by its complex nodal region. It differs from *Neocalamites* by its basally conjoined leaves which form a short sheath and having the same number of leaves as vascular bundles. Plants with *Nododendron*-type diaphragms have a greater number of vascular bundles than leaves.

The Lisarow locality is stratigraphically below that of the Beacon Hill Quarry. While the available Lisarow material conforms with the diagnosis for *T. brookvalensis*, additional material may show it to be specifically distinct.

The leafy stem (Fig. 4D) from the Beacon Hill Quarry, is preserved in a similar matrix to the leaf whorls in Fig. 4A–C. White (1986) referred this specimen to *Neocalamites hoerensis*. However, any identification is uncertain because the form of the leaf bases and their attachment to the stem cannot be determined. Also, the nodes lack the diagnostic groove and ridges of *Townroviarnites*.

Northern Hemisphere *Neocalamites carrerei* and *N. hoerensis* have been differentiated partly on the density and width of the leaves in a leaf whorl (Boureau, 1964). It is probable that Gondwana Triassic leaf-bearing stems that were assigned previously to *N. carrerei* and *N. hoerensis* should now be re-assessed for inclusion in either *Townroviarnites* or as a *Nododendron*-bearing plant.

Due to the absence of a diagnostic feature such as the ratio of the number of leaves to the number of vascular bundles, the classification of many Gondwanan Triassic leaf whorls will remain unresolved. Among such indeterminate leaf whorls are examples of linear leaves conjoining to form a short basal sheath, described by Du Toit (1927, pl. 6, fig. 6) from South Africa as *Neocalamites carrerei*; by de Cabrera (1971, fig. 6) from Argentina as *Neocalamites* sp. and by Anderson & Anderson (1985, pl. 190, fig. 1) as *Phyllothea* sp.

Genus *Paraschizoneura* Radczenko, 1955 (in Boureau, 1964)

Type species. *Paraschizoneura siberica* (Neuberg, 1948), (Radczenko, 1955 in Boureau, 1964).

Paraschizoneura jonesii n.sp.

Figs. 6A–C

- 1915 *Schizoneura*(?) cf. *africana* Feistmantel. Walkom, p. 35, pl. 3, fig. 1.
- 1924 *Schizoneura* sp. "a" Seward. Walkom, pp. 79–80, text-fig. 1.
- ?1965 *Schizoneura* sp. "a" Seward. Hill *et al.*, pl. T1, fig. 4.
- ?1973 *Schizoneura* sp. Retallack, pl. 5, figs. 4, 8.

Diagnosis. Sphenophyte foliage bearing stems with whorls of four or more elongate foliar segments each consisting of five or more linear leaves conjoined for their whole length and arranged radially around axial nodes.

Description. The holotype (Fig. 6A,B) is preserved as a foliage whorl flattened parallel to the bedding plane with the stem passing perpendicular into the matrix. Five radiating foliar lobes are attached by broad bases to an axis c. 10 mm in diameter to which a finely striated stem internode fragment is still attached; the lobes are all incomplete, to >120 mm long and to 20 mm wide; widest at half their length and tapering distally. The foliar lobes are formed from three to six leaves closely conjoined for their whole length; each leaf marked by a broad indistinct midrib and by longitudinal striations. The paratype (Fig. 6C) shows portions of two foliar whorls, one with four lobes and the other with two lobes present but the whorl is incomplete. The foliar whorls are closely associated with finely striated stems, one with an internode length of 46 mm and with c. 20 longitudinal ribs and grooves in a width of c. 10 mm. An adjacent stem is c. 0.7 mm wide with internodes c. 26 mm long.

Type material. HOLOTYPE AM F60570. PARATYPE AM F60569.

Type locality. Wave platform 600 m south of Turrimetta Head, late Early Triassic Newport Formation, Sydney Basin. GR 434 699, 1:100 000 Sydney Geological Series Sheet, 1983; 33°41'57"S 151°18'37"E.

Etymology: *jonesii*—after Mr Robert Jones, long time manager of the palaeontology collections of the Australian Museum and collector of the type specimens.

Discussion. The genus *Schizoneura*, with opposite symmetrical pairs of foliar lobes that contract basally to form a sheath, differs from *Paraschizoneura* which has four or more foliar lobes, not necessarily symmetrical and that do not contract basally to form a basal sheath although this latter feature is rarely observed. *Paraschizoneura jonesii* is

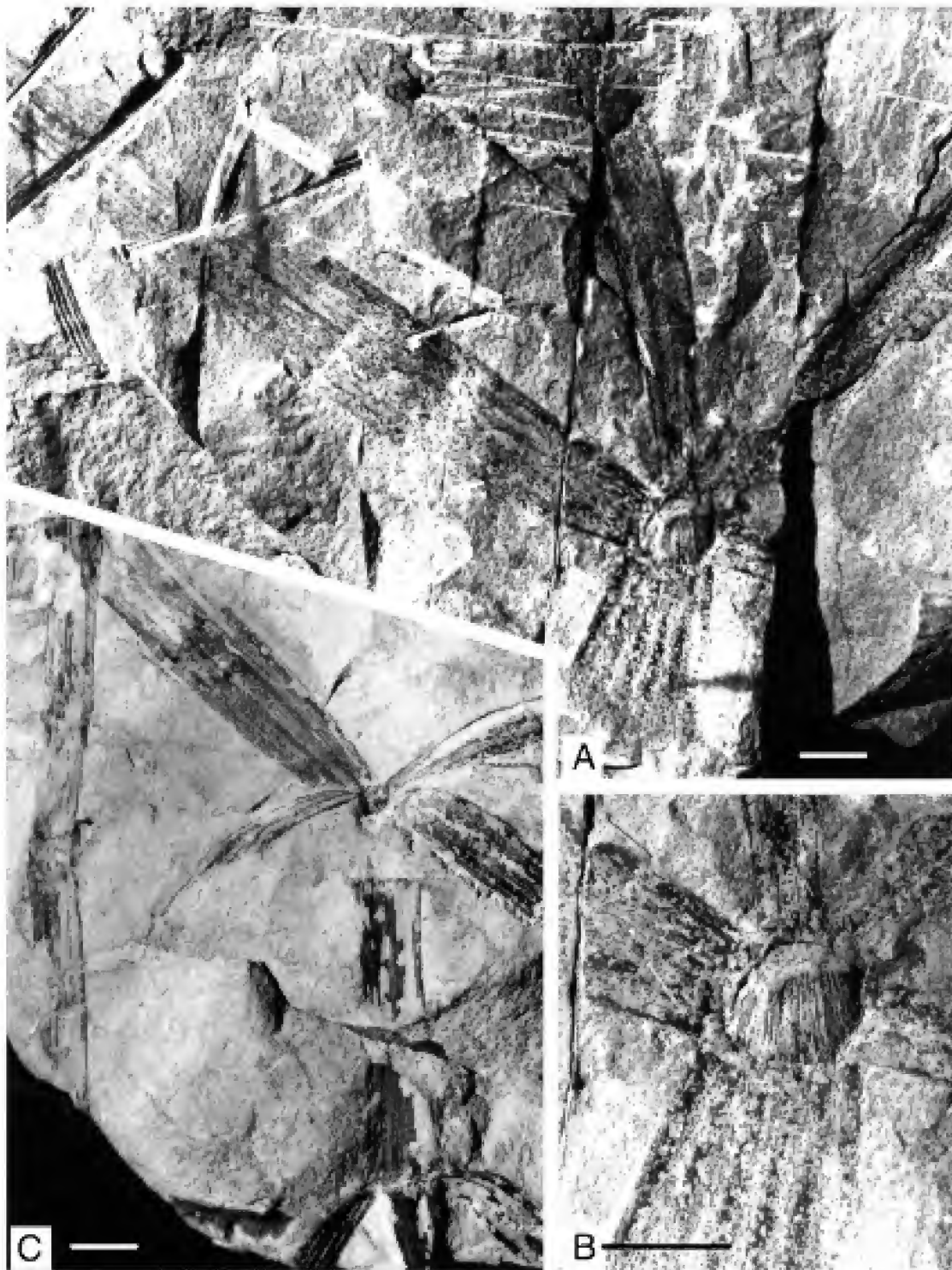


Figure 6. A–C; *Paraschizoneura jonesii* n.sp. from Turrismetta Head; A,B, holotype, AM F60570; C, paratype, AM F60569. Scale bars 1 cm.

closely comparable in gross morphology with *Schizoneura africana* Feistmantel from the Middle-Upper Permian Beaufort Group of the Karoo Basin, South Africa (Seward, 1908, text-fig. 2; Anderson & Anderson, 1985, p. 103, fig. 1 and pl. 42, figs. 1–4) and with *Paraschizoneura czezanowski* (Rasskazova, 1961 in Boureau, 1964) from the Upper Permian Tunguska Basin of Siberia (Boureau, 1964, fig. 384). Due to the wide temporal and geographical separation of these two forms and also to avoid possible erroneous assumptions of close relationships, I believe these Australian Triassic specimens are best described as a new species of *Paraschizoneura*.

Leafless equisetalean stems have no diagnostic features to justify their classification as *Schizoneura* or *Paraschizoneura*. Triassic stems referred to *Schizoneura* sp. by Walkom (1915, pls. 4,5; 1924, pl. 26, figs. 1,2), Chapman & Cookson (1926) and Hill *et al.* (1965, pl. T1, fig. 5) should be placed in *Paracalamites* Zalesky (Rigby, 1966) or rather be considered unidentifiable.

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Revisions of Genera in the *Asteron*-complex (Araneae: Zodariidae). *Asteron* Jocqué and the New Genus *Pseudasteron*

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ABSTRACT. The genus *Asteron* Jocqué is revised. It now contains 8 species: the type species *A. reticulatum* Jocqué and seven species here described as new: *A. biperforatum* n.sp., *A. grayi* n.sp., *A. hunti* n.sp., *A. inflatum* n.sp., *A. quintum* n.sp., *A. tasmaniense* n.sp. and *A. zabkai* n.sp. A key to the species is provided. The new genus *Pseudasteron* n.gen. is erected for a single new species *P. simile* n.sp.

JOCQUÉ, RUDY, & BARBARA BAEHR, 2001. Revisions of genera in the *Asteron*-complex (Araneae: Zodariidae). *Asteron* Jocqué and the new genus *Pseudasteron*. *Records of the Australian Museum* 53(1): 21–36.

The genera treated in the present paper are part of the medium size, mainly tropical spider family Zodariidae which has its highest diversity in Africa and Australia. The majority of the Australian genera, and the entire *Asteron* complex are endemic to the continent. Very little is known about the biology of these taxa but it would seem that, like most other representatives of the family, these small spiders are adapted to semi-arid areas or to regions with at least a pronounced dry season.

This is the second of a series of papers that seeks to define generic limits within the *Asteron*-complex. Initially two species were described by Jocqué (1991) in the genus *Asteron*. Baehr & Jocqué (2000) explained the reasons why this complex group has to be split. The present paper delimits the genus *Asteron* and describes several new species in it. It also erects the new genus *Pseudasteron* which has many characters in common but clearly differs from *Asteron* by characters of the secondary genitalia.

Materials and methods

The format of the descriptions follows Jocqué & Baehr (1992). All measurements are in mm. Institutions from which material was borrowed are abbreviated as follows:

- AMS Australian Museum, Sydney (M. Gray)
- KBIN Koninklijk Belgisch Instituut voor Natuurwetenschappen (L. Baert)
- MV Museum Victoria, Melbourne (C. McPhee)
- QM Queensland Museum, Brisbane (R. Raven)
- USNM United States National Museum, Smithsonian Institute, Washington (J. Coddington)
- ZSM Zoologische Sammlung des Bayerischen Staates, München (B. Baehr)

Other abbreviations include: NP, National Park; Ra, [mountain] range; Rd, road; SF, State Forest.

Systematics

Genus *Asteron* Jocqué

Asteron Jocqué, 1991: 45.

Diagnosis. Representatives of this genus are recognised by the following combination of characters: the eyes in two strongly procurved rows, resulting in a (2–4–2) situation as the PLE are situated level with the PME; tibia of male palp with shallow retrolateral concavity delimited with apophyses; bulbus with remarkably large, folded VTA and short triangular apophysis at the base of the embolus; females with poorly sclerotized epigyne showing large copulatory ducts through cuticle; copulatory ducts with fairly constant curves, leading to widely separated, poorly delimited spermathecae; dorsal abdominal pattern with five white spots on a dark background.

Description. Small to medium-sized spiders (2.50–4.00) with slightly reticulated tegument. Carapace reticulated except between fovea and eyes (Fig. 5) at its widest at level of coxae II, narrowed to 0.65 maximum width in females, to about 0.55 maximum width in males. Profile domed with highest point between fovea and PME. *Colour:* carapace, chelicerae and sternum medium to chestnut brown; legs orange to brown; abdomen dark sepia with five pale spots. Eyes in two strongly procurved rows, resulting in (2–4–2) situation, PLE situated level with PME. All eyes subequal, circular, and pale, only AME dark. AME close together and about one radius from the PME which are slightly larger. ALE twice their diameter apart. MOQ longer than wide and slightly narrower in front than in the back. Clypeus slightly convex and retreating; about 4 times the diameter of an ALE; with few hairs. Chilum double with two rather broad and short sclerites slightly wider than long, without hairs.

Chelicerae with a few hairs in front and a dense row on distal promargin; no teeth. Labium narrowed at base; sparsely haired. Gnathocoxae rather elongate; sparsely haired; with anteromesal scopula. Sternum fairly flat, triangular with straight anterior margin and slight triangular extensions between coxae. Inter- and precoxal sclerites absent. *Legs:* formula 4 1 2 3. Spination: few spines on pairs I and II, more numerous on III and IV. Tarsal claws with approximately 14 teeth on those of first leg pairs, with only about 8 teeth on those of legs III and IV. Single claw on small onychium. Trichobothria in two rows on T and in a single row on Mt and t. Hinged hairs present on TI and II. Metatarsal preening brush poorly developed, composed of chisel-shaped hairs (Fig. 6). *Abdomen:* oval, with two sigilla; in the male with a narrow dorsal scutum in anterior half and with poorly developed epiandrum. Tracheal spiracle narrow with in front of it a poorly sclerotized, slightly bulging area. Trachea from the beginning divided in four fine tubuli. Spinnerets as usual in the family; posterior pairs smaller in males than in females. Colulus represented by few hairs. *Male palp:* tibia with a frontolateral concavity delimited by dorsolateral and ventrolateral apophyses; dorsal one usually flat, ventral one strong, directed forward. Embolus long, whip-shaped with large tooth-shaped, retrolateral apophysis at base, VTA large, folded; DTA membranous; LTA short, directed retrolaterad. *Epigyne:* fairly well sclerotized but showing copulatory ducts in transparency; copulatory ducts apparently short with fairly constant trajectory, leading to widely separated, poorly delimited spermathecae. *Female palp* with slender, conical tarsus with spines on prolateral and ventral sides. Finely dentate tarsal claw turned inward over $\pm 30^\circ$.

Distribution. Eastern Australia, including Tasmania.

Type species. *Asteron reticulatum* Jocqué 1991.

Key to the species of *Asteron*

- 1 males 2
- females 6
- 2 VTA with proximal, outwards curved hook (Figs. 17, 21) 3
- proximal part of VTA rounded, without hook (Figs. 15, 19, 23) 4
- 3 proximal hook of VTA double; dorsal tibial apophysis tooth-shaped, tiny (Figs. 21–22) *A. zabkai*
- proximal hook on VTA single; dorsal tibial apophysis large, bent down and forwards (Figs. 17–18) *A. tasmaniense*
- 4 dorsal tibial apophysis sharp (Figs. 16, 24) 5
- dorsal tibial apophysis blunt, indented (Fig. 20) *A. huntii*
- 5 dorsal tibial apophysis spine-shaped as seen in ventral and frontal views, strongly tapered in lateral view; LTA a short thick hook in ventral view (Fig. 16) *A. reticulatum*

- dorsolateral tibial apophysis large and ear-shaped as seen from in front, appearing as spine-shaped with parallel margins in lateral view; LTA with straight, sharp tip, pointing outwards in ventral view (Fig. 23) *A. grayi*
- 6 entrance with two large openings in posterior half of epigyne (Fig. 37) *A. biperforatum*
- entrance hardly visible on uncleared epigyne (Figs. 31, 33, 39) 7
- 7 epigyne with one very wide depression, as broad as the epigyne, behind central opening area (Fig. 35) *A. zabkai*
- epigyne without well marked depression (Fig. 27) 8
- 8 internal structure visible through cuticle not reaching posterior margin of epigyne (Figs. 25, 27) 9
- internal structure visible through cuticle reaching posterior margin of epigyne (Figs. 29, 31, 33, 39) 10
- 9 projection of copulatory duct in transparency forming an almost complete circle (Fig. 25) *A. reticulatum*
- projection of copulatory duct in transparency with a large interruption in front and dark circular areas aborally (Fig. 27) *A. tasmaniense*
- 10 posterior margin of epigyne straight or indented; central part of copulatory ducts straight 11
- posterior margin of epigyne convex; central part of copulatory ducts curved 12
- 11 posterior margin of epigyne slightly concave (Fig. 33) *A. quintum*
- posterior margin of epigyne straight (Fig. 31) *A. inflatum*
- 12 epigyne with diamond-shaped pale central area just in front of posterior margin (Fig. 39) *A. grayi*
- epigyne without diamond-shaped pale central area but with dark adjacent circular areas near posterior margin (Fig. 29) *A. huntii*

***Asteron reticulatum* Jocqué, 1991**

Figs. 1–4, 5–8, 13, 15–16, 27–28, 45

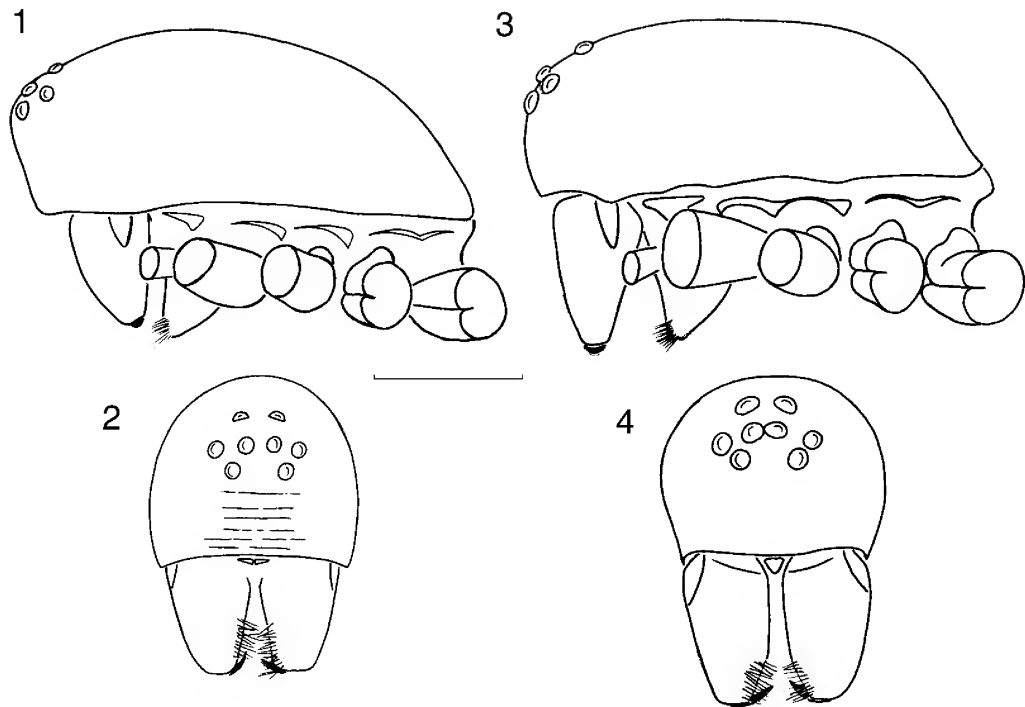
Asteron reticulatum Jocqué, 1991: 46 (descr. ♂ ♀).

Type material re-examined. HOLOTYPE ♂: Australia, New South Wales, Bondi SF, S of Bombala, woodlot 1, 37°08'S 149°09'E, 15.x.1980, G. Gowing *et al.* (AM KS11310); 1 ♂, Wiola Creek Fire Trail, Badja SF, 36°05'24"S 149°34'51"E, 13.iii.1999, J. Tarnawski, S. Lassau (AM KS55872); 1 ♂, Tuross River Rd, Badja SF, 36°12'17"S 149°30'07"E, 13.iii.1999, L. Wilkie, R. Harris, H. Smith (AM KS55880); 1 ♀, Badja SF Rd, Badja SF, 36°10'51"S 149°29'45"E, as previous (AM KS55883).

New material examined. VICTORIA: 1 ♂, site 513.04, Sardine Coupe, 37°25'S 148°31'E, 9–15.iv.1992, pitfall traps, upslope, R. Coy (MV K3802); 2 ♀ ♀, as previous (MV K3803); 1 ♀, 9–15.iv.1992, as previous (MV K3812); 1 ♀, 11–18.ii.1992,

midslope, as previous (MV K3806); 1 ♂, 18–25.ii.1992, as previous (MV K3820); 1 ♀, 1 juvenile, site 513.06, as previous, 11–18.ii.1992 (MV K3810); 1 ♀, 10–15.v.1992, gully, as previous (MV K3851); 4 ♂ ♂, 1 ♀, site 515.07, Rich-Murrungowar Coupe, 37°34'S 148°38'E, 29.x–6.xi.1991, pitfall traps, gully, R. Coy (MV K3815); 1 ♀, as previous (MV K3815); 1 ♂, site 509.08, as previous, 37°34'S 148°39'E, 2.x–5.xi.19912, midslope (MV K3795); 1 ♀, Upper Yarra Survey, site 6, 11.0 km NE McMahon Ck, 37°39'S 145°56'E, 14–24.xi.1988, L. Lumsden (MV K3766); 4 ♂ ♂, 3 ♀ ♀, Punchbowl, 41°27'S 147°10'E, 7.iv.1930, V. Hickman (AM KS30322); 2 ♂ ♂, 7 ♀ ♀, as previous, 28.v.1918 (AM KS30328).

Diagnosis. Males of this species are recognised by the shape of the tibial apophysis of which the sharp tip points downward (turned forward in *A. tasmaniense*); the tooth at the base of the embolus is fairly narrow and clearly concave along its prolateral side. Females can be recognised by the details of the epigyne in which the distal part of the copulatory



Figures 1–4. *Asteron reticulatum* Jocqué: 1, female carapace, profile; 2, eye region frontal view. *Pseudasteron simile* n.gen., n.sp.: 3, female carapace, profile; 4, eye region frontal view. Scale = 0.5 mm.

ducts almost completely encircle the proximal part.

Description. *Male*: total length 2.72; carapace 1.54 long, 1.01 wide, patella I+tibia I 1.13. *Colour*: carapace dark chestnut brown; chelicerae medium brown; sternum reddish brown; legs medium brown with femora distinctly darker than remainder of legs. Abdomen: dorsum dark sepia with five white spots: one pair in front, one pair in the middle and a single spot in front of the spinnerets; sides dark; venter with a longitudinal pale patch behind the epigastric fold, and a big white spot on either side, half way between spinnerets and epigastric fold. *Eyes* (measurements in mm): a, 0.07; b, 0.08; c, 0.07; d, 0.09; e, 0.01; f, 0.04; g, 0.04; h, 0.10; AL–AL, 0.12. MOQ:AW = 0.78 PW, AW = 0.60 L. Clypeus 0.32 high, slightly convex. *Leg spination*:

	F	P	T	Mt
I	d1	–	–	–
II	d1	–	–	v1
III	d1	pl1	pl2*d2*v1	4 disp dw5
IV	d2*	pl1rl1	pl2*d2*rl2*v3*	5 disp dw6

Male palp (Figs. 7, 8, 15, 16): tibia with sharp, downpointing dorsolateral and blunt ventrolateral apophysis delimiting dorsolateral concavity; embolus whip-like and twisted; big tooth at base with concave prolateral rim in ventral view; VTA massive and complex; DTA membranous: stalk thin, distal part widened with transverse distal appendage; LTA recurved in ventral view.

Female: total length 2.84 (2.84–3.42), carapace 1.66 (1.54–1.66) long, 1.05 (1.00–1.06) wide. *Colour*: very much as in the male but with a more reddish tinge all over; abdomen without scutum. *Eyes* as in the male. *Leg spination*:

	F	P	T	Mt
I	d1	–	–	–
II	d1	–	–	–
III	d1	pl1	pl2*d2*v1	5 disp dw4
IV	d2*	pl1rl1	pl2*d2*rl2*v2*	6 disp dw5

Epigyne (Figs. 13, 25, 26): rather simple: a sclerotized rectangular plate, strongly sclerotized along posterior margin, with a small central lip behind a tiny epigynal opening; opening slit-shaped; copulatory ducts visible through tegument: distal part (oral side) almost completely encircle proximal (caudal) part.

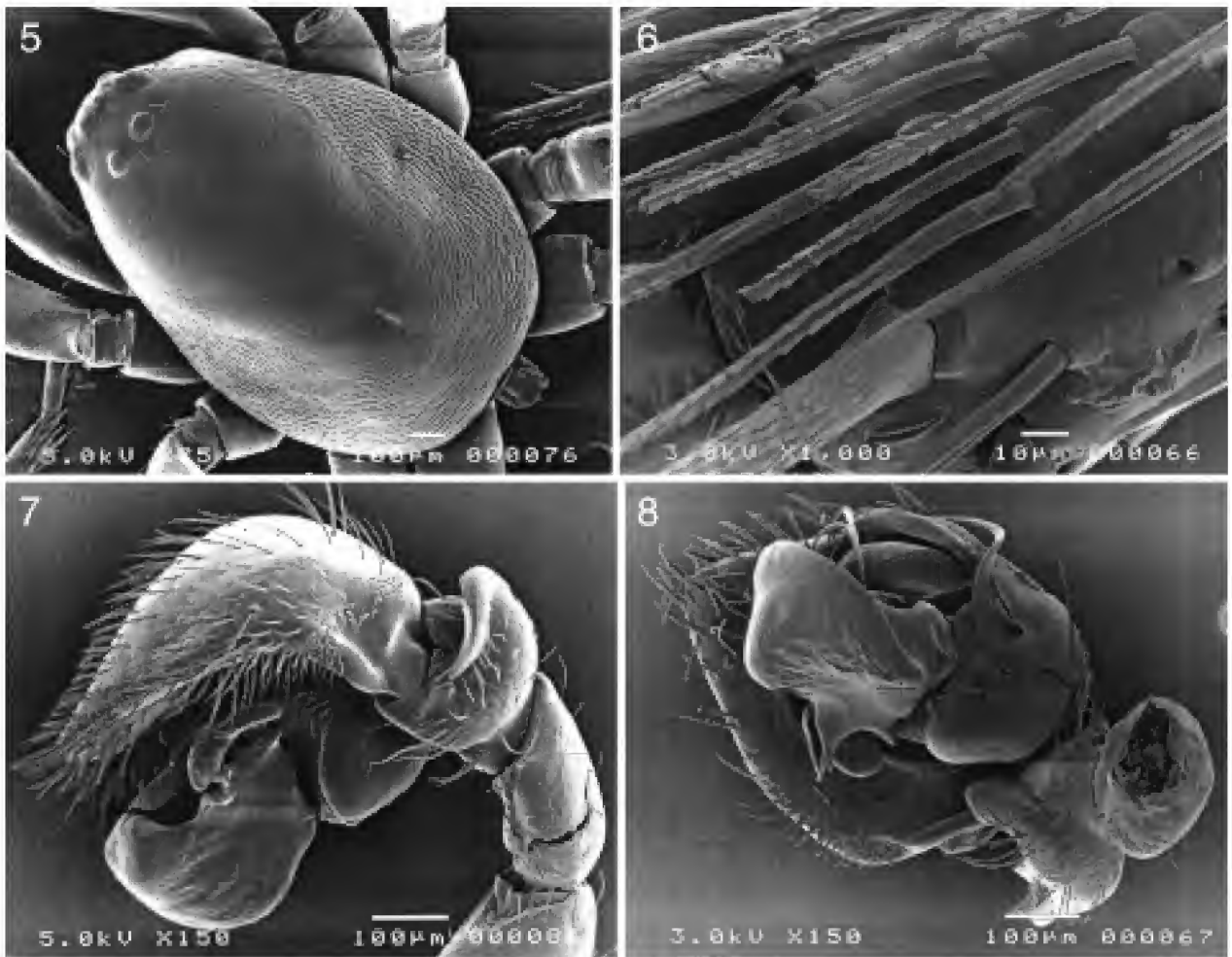
Variation. TL: 2.54–3.08, carapace length 1.42–1.58, width 0.94–1.02.

Distribution. New South Wales, Queensland (Fig. 45).

***Asteron tasmaniense* n.sp.**

Figs. 17, 18, 27, 28, 45

Type material. HOLOTYPE ♀: Tasmania, Domain, 42°53'S 147°19'E, 24.viii.1942, in cranberry tussocks, V. Hickman (AM KS30326). PARATYPES: Tasmania: 3 ♂♂, 6 ♀♀, same data as holotype; 2 ♂♂, 3 ♀♀, 3.viii.1968, as previous (AM KS30327); 2 ♀♀, 16.viii.1943, in grass tussocks, as previous (AM KS30336); 1 ♂, 1.ix.1934, as previous (AM KS30353); 1 ♀, v.1948, as previous (AM KS30337); 1 ♀, Trevallyn 41°27'S 147°10'E, 12.xi.1932, in grass tussocks, V. Hickman (AM KS30334); 2 ♀♀, 26.v.1928, in moss, as previous (AM KS30322); 1 ♀, Ridgeway, 42°56'S 147°17'E, 14.v.1948, C. Oke (AM KS30343); 1 ♂, Punchbowl, 41°27'S 147°10'E, 1.vi.1931, from moss, V. Hickman (AM KS30330).



Figures 5–8. *Asteron reticulatum* Jocqué: 5, female carapace, dorsal view; 6, chisel-shaped hairs of preening brush on MtIV; 7, male palp, retrolateral view; 8, male palp, ventral view.

Other material. None.

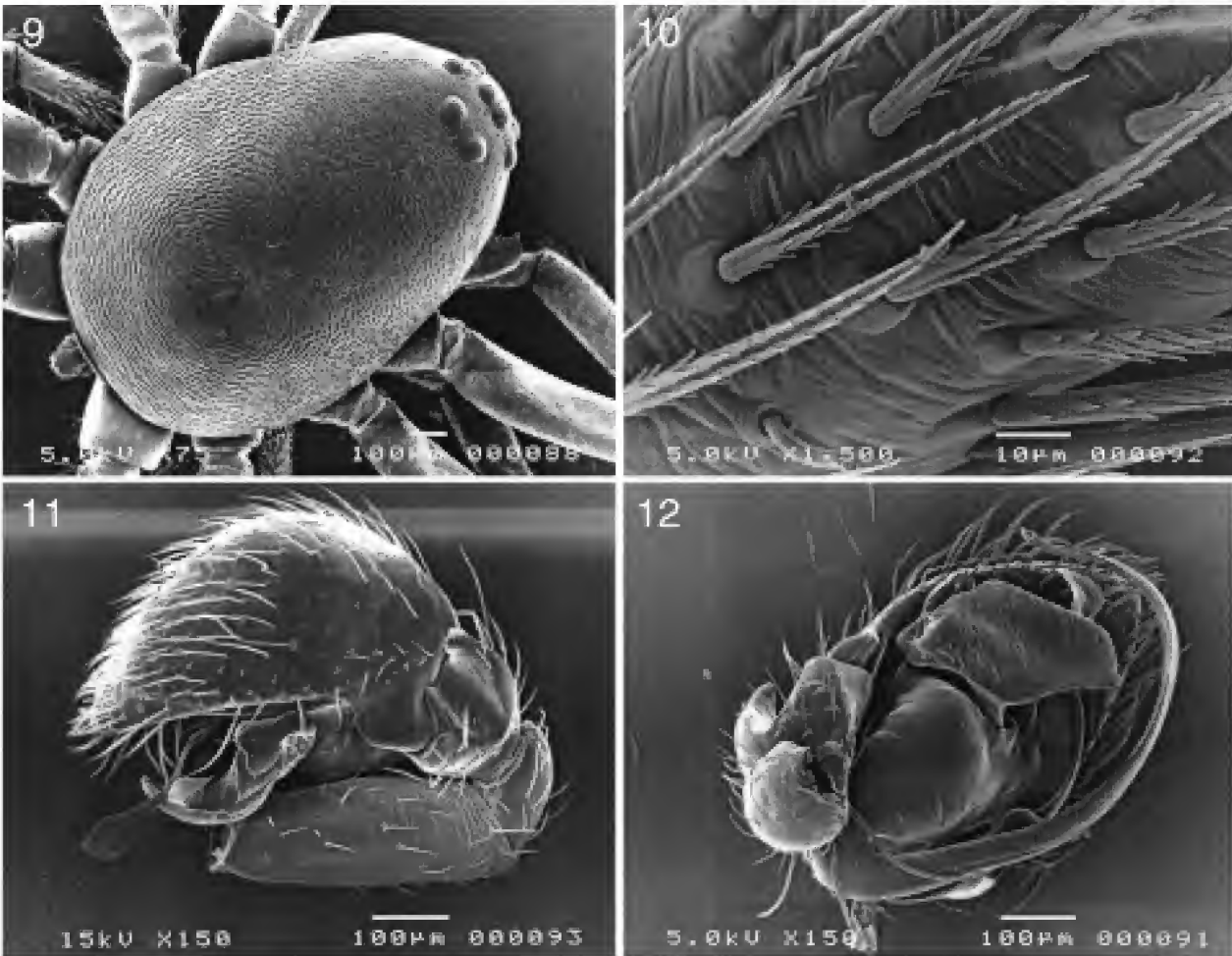
Diagnosis. Males of this species are recognised by the retrolateral tibial apophysis in which the dorsal prong is sharp and clearly curved forward. Females may be recognised by shape of the copulatory ducts in the epigyne: on either side, the oval outline of the copulatory ducts is widely interrupted in front.

Description. *Male* (paratype AM KS30326): total length 2.74; carapace 1.30 long, 0.92 wide; tibia+patella I 1.04. *Colour:* carapace, chelicerae and sternum uniform medium brown; sternum reddish brown; legs uniform yellowish brown; abdomen: dorsum dark sepia with five white spots: one pair in front, one pair in the middle and a single spot in front of the spinnerets; sides dark, with large ventrolateral white spot continuing on venter; venter with one poorly defined paler spot behind epigastric fold and yellow spot in front of spinnerets. Carapace finely reticulated. *Eyes* (measurements in mm): a, 0.06; b, 0.05; c, 0.06; d, 0.07; e, 0.02; f, 0.03; g, 0.06; h, 0.08; AL–AL, 0.12. MOQ:AW = 0.77 PW; AW = 0.63 L. *Leg spination:*

	F	P	T	Mt
I	d1	–	–	–
II	d1	–	–	v1
III	d1	pl1	pl2*d2*v1	2 disp dw5
IV	d2*	pl1rl1	pl2*d2*rl2*v3*	6 disp dw5

Hinged hairs: TI d1, TH d1. *Male palp* (Figs. 17, 18): tibia with retrolateral concavity, delimited by two apophyses: ventrolateral apophysis gutter-shaped with sharp, procurved proximal prong; ventrolateral apophyses blunt, produced under rim of cymbium; cymbium with flat flange delimited on dorsal side by thick ridge; embolus fairly long and twisted with large, embolar apophysis; VTA massive and complex; LTA spine-shaped; DTA membranous: root thin, distal part broad, rounded.

Female (holotype): total length 3.10; carapace 1.50 long, 0.94 wide; tibia+patella I 0.98. *Colour:* as in male except sides of abdomen with several oblique white patches and venter almost entirely pale but a faint large darker median band touching the yellow spot in front of the spinnerets. Carapace finely reticulated. *Eyes* (measurements in mm): a, 0.06; b, 0.06; c, 0.07; d, 0.07; e, 0.02; f, 0.04; g, 0.04; h, 0.09; AL–AL, 0.14. MOQ:AW = 0.77 PW; AW = 0.70 L. *Leg spination:*



Figures 9–12. *Pseudasteron simile* n.gen., n.sp.: 9, female carapace, dorsal view; 10, chisel-shaped hairs of preening brush on MtIV; 11, male palp, retrolateral view; 12, male palp, ventral view.

	F	P	T	Mt
I	d1	–	pl1	–
II	d1	–	–	v1
III	d1	pl1	pl2*d2*v1	2 disp dw5
IV	d2*	pl1rl1	pl2*d2*rl2*v2*	5 disp dw5

Hinged hairs: TI d1, TII d1. *Epigyne* (Figs. 27, 28): a poorly sclerotized oval area with strongly sclerotized posterior rim with pointed central tip; copulatory ducts showing through tegument have a roughly oval outline, widely interrupted in front. Delimitation of spermathecae unclear.

Variation. Colour pattern and spination very stable, extremities of leg joint sometimes somewhat paler: male carapace length and width vary between 1.40 and 1.24, 0.96 and 0.90; female carapace between 1.30 and 1.50, 0.86 and 0.96.

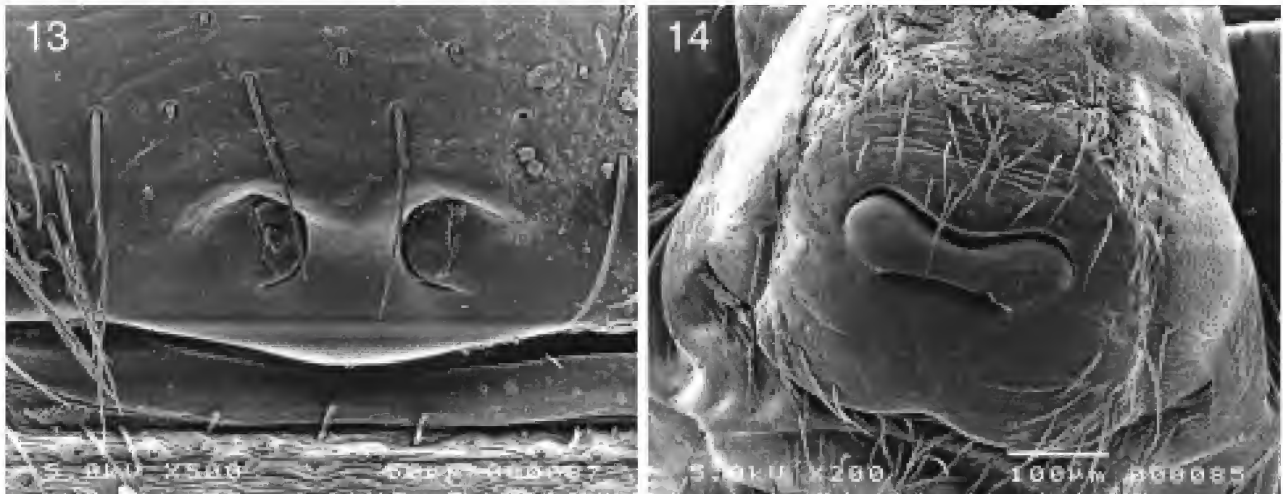
Distribution. Known only from southern Tasmania (Fig. 45).

Etymology. The species name is an adjective derived from the type locality of the species.

Asteron hunti n.sp.

Figs. 19, 20, 29, 30, 45

Type material. HOLOTYPE ♂: Australia, New South Wales, Abercrombie Caves, near Bushrangers Cave, 33°54'S 149°21'E, x.1989, G. Hunt (AM KS22479). PARATYPES: NEW SOUTH WALES: 1♂, Bungonia Caves area near Information Centre, 34°48'S 150°01'E, xi.1989, G. Hunt, (AM KS22563); 1♂, 1♀, x.1989, as previous (AM KS22581); 1♂, as previous (AM KS22582); 1♂, i.1990, as previous (AM KS22738); 2♂♂, 2♀♀, Kanangra-Boyd NP, Blood Filly Ck near Jenolan Caves, 33°51'S 150°03'E, 27.iii.1976, Gray, Hunt & McDougall (AM KS29874); 1♂, Royal NP, upper causeway ca. 100 m from road, 34°08'S 151°04'E, 12.iii.1991 (AM KS27891); 1♀, Munmorah State Rec., 33°12'26"S 151°34'37"E, 16.xii.1996, L. Wilkie (AM KS55947); 1♂, as previous (AM KS55920), 1♂, as previous (AM KS55926); 1♂, as previous (AM KS55971); 1♂, as previous (AM KS55985); 1♂, as previous (AM KS55996); 1♂, as previous (AM KS55999); 1♂, as previous (AM KS55978); 1♀, Myall Lakes NP, 32°34'45"S 142°17'27"E, 14.xi.1996, L. Wilkie (AM KS55967); 1♂, as previous, 32°37'56"S 152°12'27"E, 10.x.1997, L. Wilkie (AM KS55995); 1♂, Wyrabalong NP, 33°16'51"S 151°32'37"E, 23.v.1998, L. Wilkie (AM KS55062). AUSTRALIAN CAPITAL TERRITORY: 1♀, Brindabella Mountains, near Uriarra Ck, ca. 15 km W. Canberra, 6.viii.1990, 700 m, berlese, leaf litter from *Eucalyptus* forest, C. Griswold & T. Meikle (USNM).



Figures 13–14. Epigynes, ventral view. 13, *Asteron reticulatum* Jocqué. 14, *Pseudasteron simile* n.gen., n.sp.

Other material. None.

Diagnosis. Males of this species are recognised by the retrolateral tibial apophysis in which the dorsal prong is curved forward and slightly indented. Females may be recognised by shape of the copulatory ducts in the epigyne: on either side the oval outline of the copulatory ducts, visible through cuticle, is only slightly interrupted in front.

Description. *Male* (holotype): total length 2.90; carapace 1.40 long, 0.94 wide; tibia+patella I 0.96. *Colour:* carapace and chelicerae uniform orange brown; sternum reddish brown; legs uniform yellowish brown; abdominal pattern poorly defined: dorsum dark sepia with five white spots: one spot on either side adjacent with a narrow, pale yellow scutum, one pair in the middle and a single spot in front of the spinnerets; sides dark; venter with two large pale spots behind epigastric fold and yellow spot in front of spinnerets. Carapace and sternum with fairly coarse reticulations. *Eyes* (measurements in mm): a, 0.07; b, 0.06; c, 0.08; d, 0.08; e, 0.02; f, 0.02; g, 0.02; h, 0.06; AL–AL, 0.12. MOQ:AW = 0.88 PW; AW = 0.72 L. *Leg spination:*

	F	P	T	Mt
I	d1	–	pl1	–
II	d1	–	–	v1
III	d1	pl1	pl2*d2*v1	4 disp dw5
IV	d2*	pl1rl1	pl2*d2*rl2*v3*	5 disp dw5

Hinged hairs: TI d1, TII d1. *Male palp* (Figs. 19, 20): tibia with retrolateral concavity, delimited by two apophyses: ventrolateral apophysis pointing forward, blunt, produced under proximal part of cymbial flange; cymbium with flat flange; embolus fairly long and twisted with large, triangular basal apophysis, with clearly concave prolateral side; VTA massive and complex; LTA short, bifurcated: ventral part ridged, dorsal part spine-shaped; DTA membranous, roughly triangular: strongly widened from narrow base.

Female paratype: total length 3.78; carapace 1.48 long, 1.00 wide; tibia+patella I 1.04. *Colour:* as in male except legs with pale patellae and extremities of femora and tibiae; abdomen without scutum pale spots smaller than in male;

sides of abdomen with several oblique white patches and venter almost entirely pale but with two faint longitudinal darker median bands in front of posterior yellow spot. Carapace and sternum reticulated. *Eyes* (measurements in mm): a, 0.06; b, 0.08; c, 0.08; d, 0.10; e, 0.02; f, 0.04; g, 0.04; h, 0.09; AL–AL, 0.12. MOQ:AW = 0.70 PW; AW = 0.58 L. *Leg spination* and *hinged hairs* exactly as in male. *Epigyne* (Figs. 29, 30): a poorly sclerotized oval area with strongly sclerotized, accolade-shaped posterior rim; copulatory ducts showing through tegument have a roughly oval outline, slightly interrupted in front. Delimitation of spermathecae unclear.

Variation. Colour pattern and spination stable; male carapace length and width vary between 1.38 and 1.42, 0.92 and 0.96; female carapace between 1.40 and 1.48, 0.94 and 0.96.

Distribution. Known only from New South Wales (Fig. 45).

Etymology. The species name is a patronym in honour of the collector of the type.

Asteron inflatum n.sp.

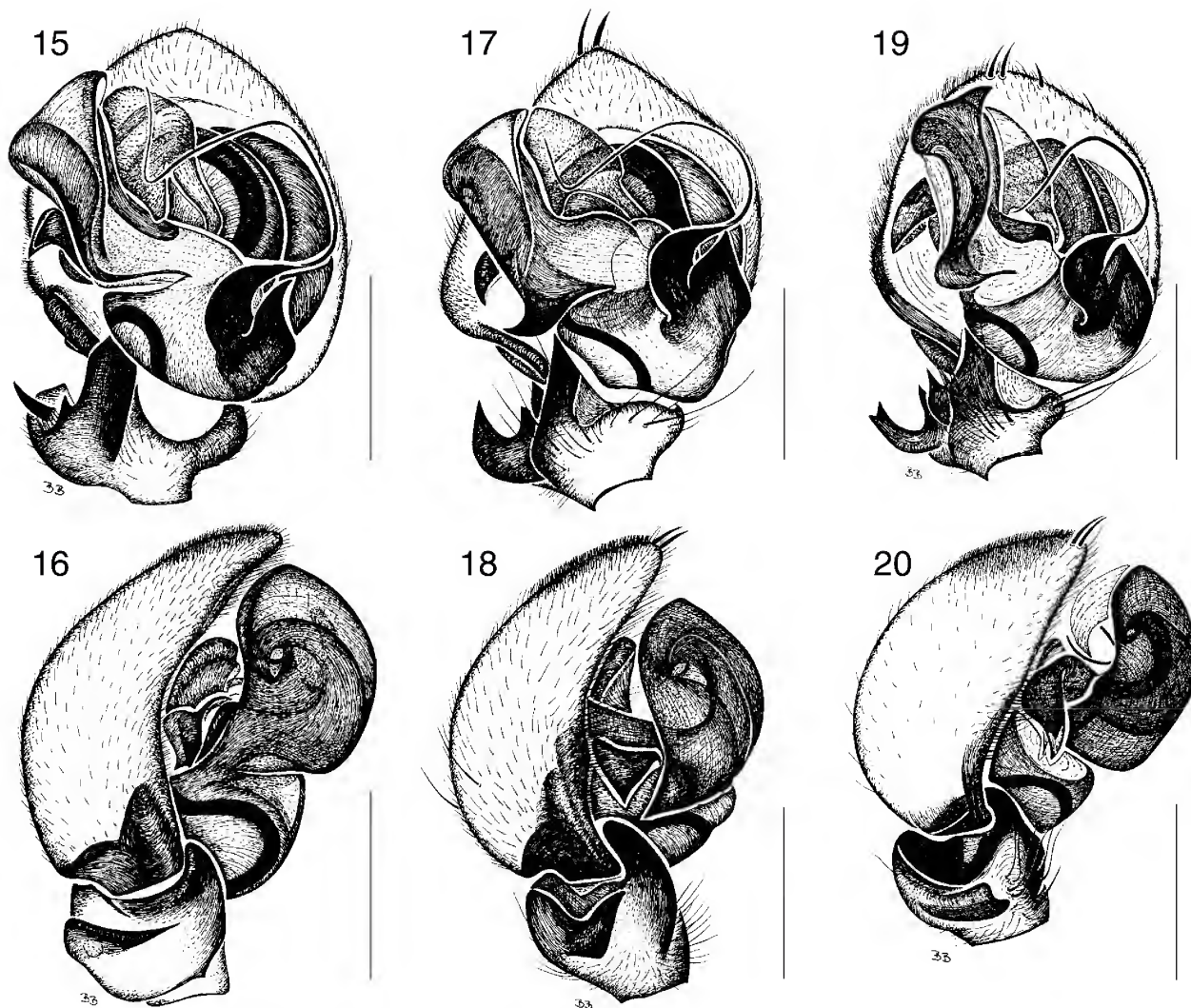
Figs. 31, 32, 45

Type material. HOLOTYPE ♀: Australia, Victoria, reserve, Dingley Road, 37°58'S 145°08'E, 10–13.i.1991, pitfall trap, S. Larwill (MV K3772).

Other material. None.

Diagnosis. Females of this species are recognised by the course of the copulatory ducts in the transparent cuticle of the epigyne: the mesal part of the ducts is straight whereas the lateral part is clearly looped which is not visible in the other species.

Description. *Female* (holotype): total length 3.96; carapace 1.56 long, 1.00 wide; tibia+patella I 1.02. *Colour:* carapace, chelicerae and sternum uniform orange brown; legs yellowish



Figures 15–20. Male palps, ventral view (top), lateral view (bottom). 15–16, *Asteron reticulatum* Jocqué; 17–18, *A. tasmaniense* n.sp.; 19–20, *A. huntii* n.sp. Scale = 0.25 mm.

brown with patellae and extremities of tibiae paler; abdomen: dorsum dark sepia with five white spots: one pair in front, one pair in the middle and a single spot in front of the spinnerets; sides dark with one large white spot continuing on venter and two oblique stripes near the back; venter pale with two narrow, interrupted longitudinal dark bands. Carapace and sternum finely reticulated. *Eyes* (measurements in mm): a, 0.05; b, 0.07; c, 0.07; d, 0.06; e, 0.02; f, 0.02; g, 0.05; h, 0.10; AL–AL, 0.14. MOQ:AW = 0.63 PW; AW = 0.60 L. *Clypeus* = 0.26 mm or 3.7 times diameter of ALE; chilum double, each part 0.06 high, 0.14 wide. *Leg spination*:

	F	P	T	Mt
I	d1	–	–	–
II	d1	–	–	v1
III	d1	pl1	pl2d2*v1	4 disp dw4
IV	d2*	pl1rl1	pl2*d2*rl2*v3*	5 disp dw4

Hinged hairs: TI d1, TII d1. *Epigyne* (Figs. 31, 32): poorly sclerotized oval area with slightly darker, straight posterior rim. Proximal part of copulatory ducts straight, distal part strongly sinuous and clearly looped ending in

well-delimited spermathecae.

Male unknown.

Distribution. Known only from type locality (Fig. 45).

Etymology. The species name is an adjective (Latin *inflatus* = swollen) and refers to the well delimited spermathecae.

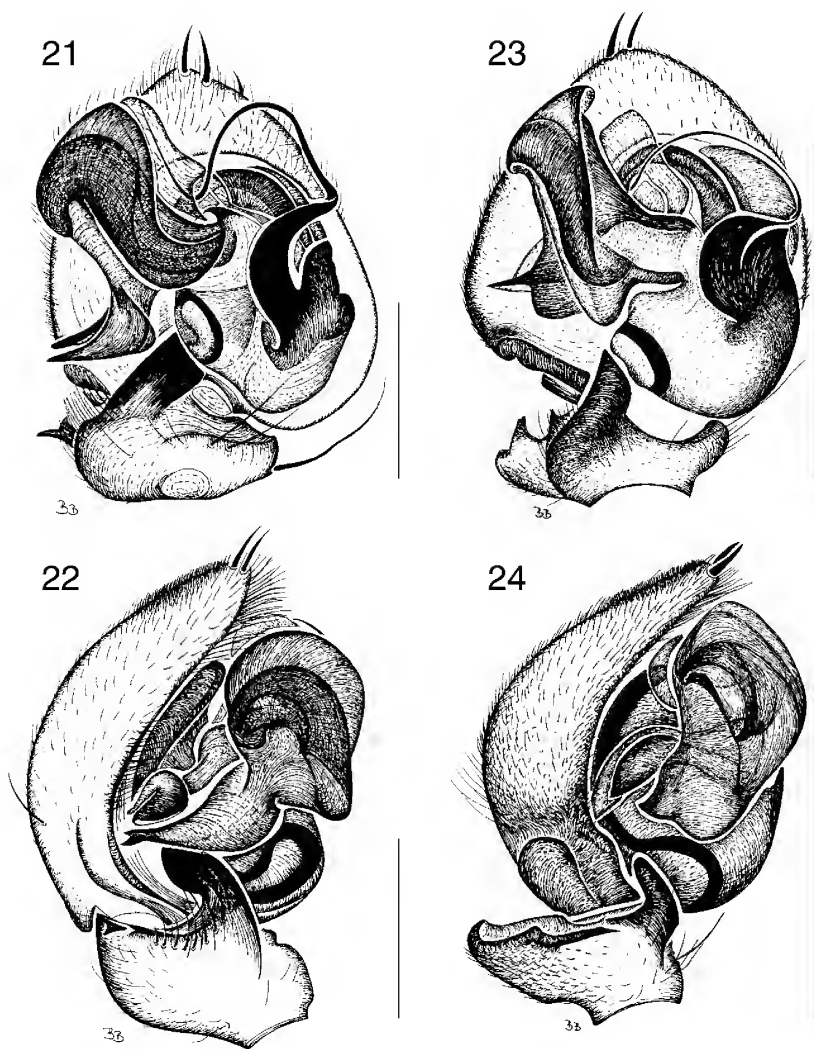
Asteron quintum n.sp.

Figs. 33, 34, 45

Type material. HOLOTYPE ♀: Australia, Victoria, Dartmouth Survey, Stoney Creek, 36°34'S 147°35'E, 13.ix.1973 (MV K3828).

Other material. None.

Diagnosis. Females of this species are recognised by the course of the copulatory ducts under the transparent cuticle: the mesal part of the ducts is straight whereas the lateral part is slightly sinuous and curved forward.



Figures 21–24. Male palps, ventral view (top), lateral view (bottom). 21–22, *A. zabkai* n.sp.; 23–24, *A. grayi* n.sp. Scale = 0.25 mm.

Description. *Female* (holotype): total length 2.88; carapace 1.48 long, 0.96 wide; tibia+patella I 0.96. *Colour:* carapace, chelicerae and sternum uniform orange brown; legs yellowish brown with patellae and extremities of tibiae paler; abdomen: dorsum dark sepia with five white spots: one pair in front, one pair in the middle and a single spot in front of the spinnerets; sides dark with three oblique stripes, the anterior one continuing into large white spot on venter. Venter pale with two fairly wide longitudinal dark bands. Carapace and sternum finely reticulated. *Eyes* (measurements in mm): a, 0.05; b, 0.08; c, 0.07; d, 0.06; e, 0.02; f, 0.02; g, 0.04; h, 0.08; AL–AL, 0.12. MOQ:AW = 0.66 PW; AW = 0.50 L. *Chypeus* = 0.22 mm or 2.7 times diameter of ALE; chilum double, each part 0.06 high, 0.14 wide. *Leg spination:*

	F	P	T	Mt
I	d1	–	pl1	–
II	d1	–	–	v1
III	d1	pl1	pl2*d2*v1	4 disp dw4
IV	d2*	pl1rl1	pl2*d2*rl2*v3*	5 disp dw4

Hinged hairs: TI d1, TII d1. *Epigyne* (Figs. 33, 34): poorly sclerotized oval area with slightly darker, sinuous posterior rim. Proximal part of copulatory ducts visible through cuticle almost straight, distal part strongly recurved and slightly procurved near anterior turn; ending in well-developed spermathecae.

Male unknown.

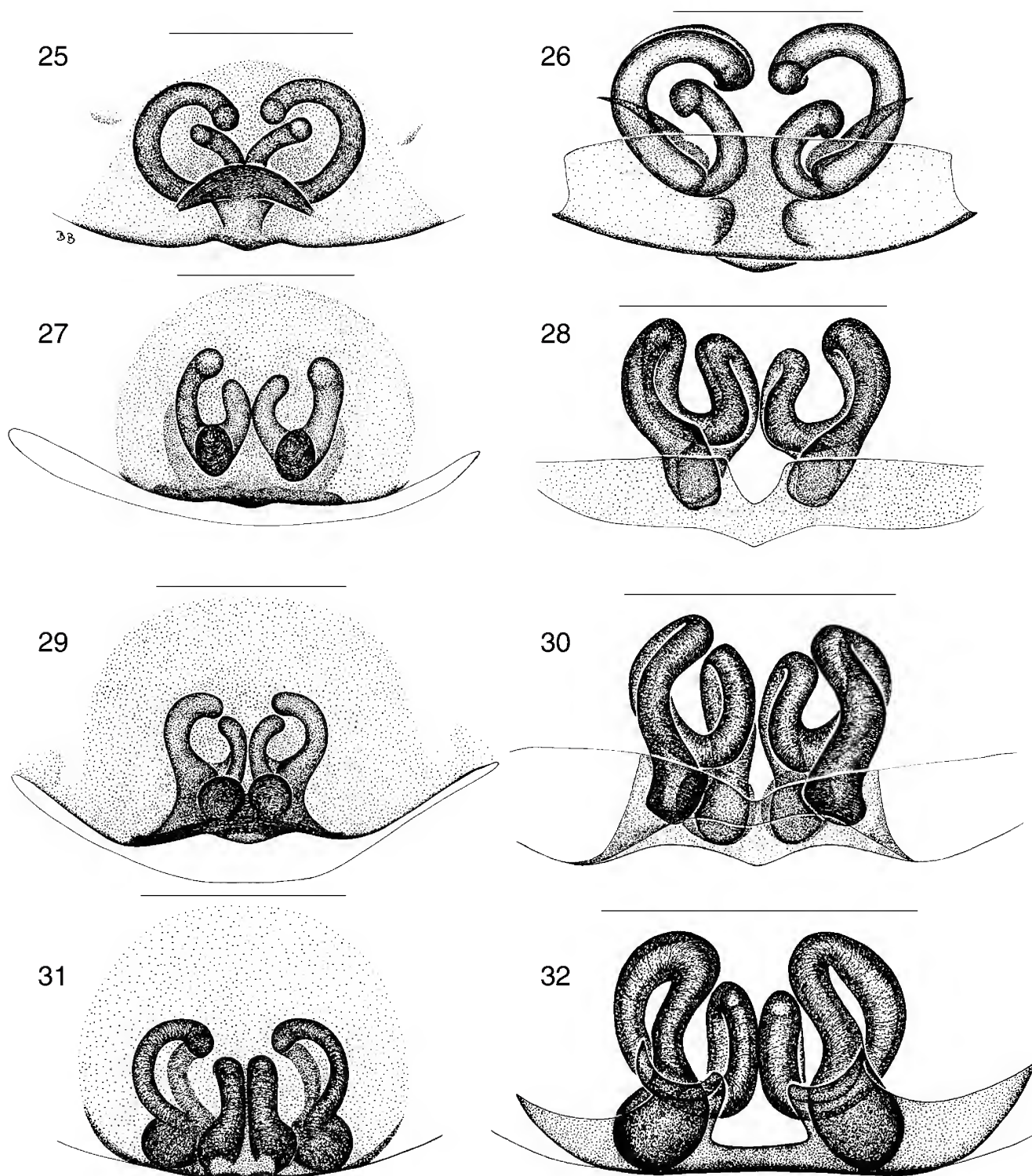
Distribution. Known only from type locality (Fig. 45).

Etymology. The species name is an adjective (Latin *quintus* = the fifth) as this is the fifth species described in *Asteron* s.str.

Asteron zabkai n.sp.

Figs. 21, 22, 35, 36, 45

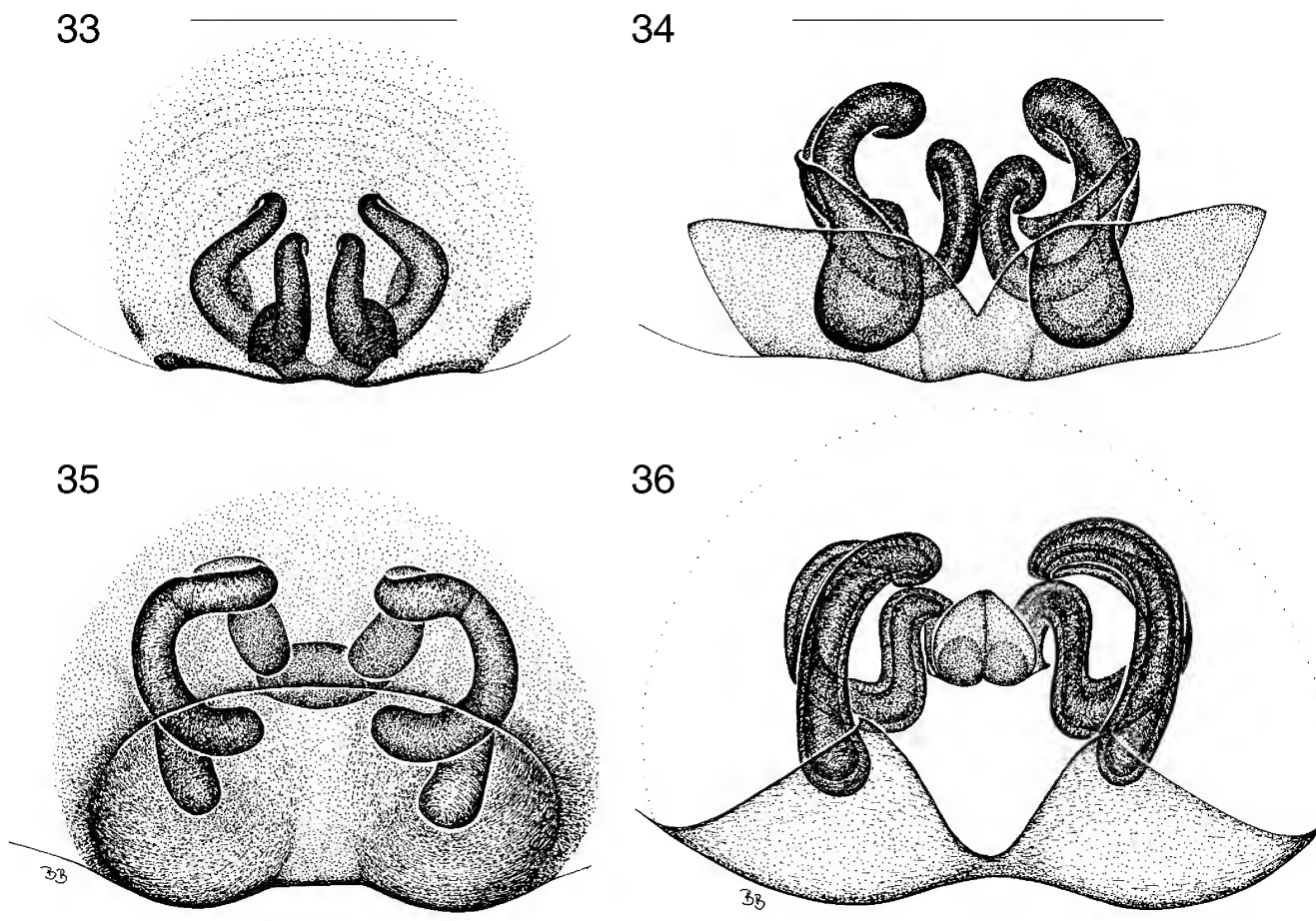
Type material. HOLOTYPE ♂: Australia, New South Wales, Royal NP, upper causeway, 34°08'S 151°04'E, 25.viii.1988, M. Zabka, C. Horseman & L. Sanchez (AM KS27938). PARATYPES: NEW SOUTH WALES: 1 ♂, Royal NP, upper causeway, ca. 100 m from road, 12.iii.1991, C. Horseman & B. Haren (AM KS27891); 1 ♀,



Figures 25–32. Epigynes, ventral view (left), dorsal view of cleared epigyne (right). 25–26, *Asteron reticulatum* Jocqué; 27–28, *A. tasmaniense* n.sp.; 29–30, *A. huntii* n.sp.; 31–32, *A. inflatum* n.sp. Scale = 0.25 mm.

Enfield SF, Dodds Fire Trail, about 3 km from Enfield Road, 910 m, 31°24'S 151°52'E, 4.ii–9.iv.1993, M. Gray & G. Cassis (AM KS039111); 1 ♀, as previous, about 2 km from Enfield Road, 930 m, 31°23'S 151°52'E (AM KS039109); 2 ♂♂, 4 ♀♀, Wahroonga Fox Valley, 17.xi.1979, B. Henke (AM KS5617); 7 ♂♂, 5 ♀♀, as previous (AM KS5593; 1 ♂, 1 ♀ in ZSM; 1 ♂, 1 ♀ in KBIN); 2 ♀♀,

Chichester SF, Mt Allyn Road, N of Shellbrook Forest Rd, 32°08'S 151°27'E, 770 m, 4.ii–9.iv.1993, M. Gray & G. Cassis (AM KS39141); 2 ♀♀, as previous, 2.3 km N of Kuruah R on Kuruah R Rd, 32°05'S 151°43'E, 520 m, NPWS Survey (AM KS039815); 3 ♀♀, as previous, 1.3 km N of Kuruah R on Kuruah R Rd, 32°05'S 151°43'E, 520 m NPWS Survey (AM KS039816); 1 ♀, as previous, 300 m off Mt



Figures 33–36. Epigynes, ventral view (left), dorsal view of cleared epigyne (right); 33–34, *A. quintum* n.sp.; 35–36, *A. zabkai* n.sp. Scales (mm) = 0.5 (33), 0.25 (34) and 0.1 (35, 36).

Allyn Rd, 32°09'S 151°27'E, 580 m (AM KS039141); 1 ♀, as previous, S of Mt Allyn Road, Allyn River Forest, N of Shellbrook Forest Rd, 32°09'S 151°28'E, 385 m, (AM KS039142); 1 ♀, Padmans Rd near intersection of Pole Dump Rd, 31°36'S 152°10'E, 730 m, NPWS Survey, 4.ii–9.iv.1993, M. Gray & G. Cassis (AM KS039409); 1 ♂, Mountain trail, 0.8 km of junction with Kunungra Rd, 32°08'S 151°45'E, 300 m, NPWS Survey, 4.ii–9.iv.1993, M. Gray & G. Cassis (AM KS039818); 1 ♂, Mountain trail, 0.8 km of junction with Kunungra Rd, 32°08'S 151°45'E, 300 m, NPWS Survey, 4.ii–9.iv.1993, M. Gray & G. Cassis (AM KS039817); 3 ♀ ♀, Westerly branch of Kunderang Station Ck, 30°48'S 152°06'E, 320 m, 4.ii–9.iv.1993, M. Gray & G. Cassis (AM KS039408); 2 ♀ ♀, Bulga SF, Homewoods Rd, 2.8 km W of Knodingbul Rd, 31°37'S 152°07'E, 690 m, NPWS Survey, 4.ii–9.iv.1993, M. Gray & G. Cassis (AM KS039410); 1 ♀, Coomerang Rd, Dampier SF, 36°06'46"S 149°59'39"E, 10.iii.1999, L. Wilkie, R. Harris, H. Smith (AM KS055884).

Other material. None.

Diagnosis. Males of this species are recognised by the retrolateral tibial apophysis in which the ventrolateral part is very large and provided with a short sharp tip pointing down; the female is easily recognised by the very wide depression behind the epigynal opening covering the entire width of the epigyne.

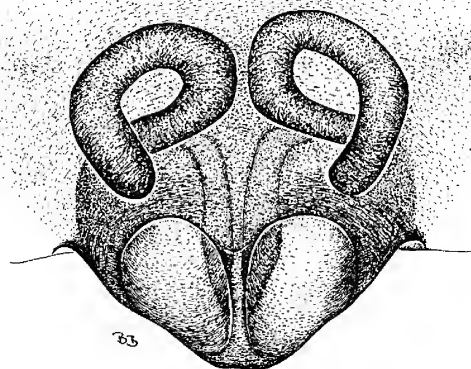
Description. *Male* (holotype): total length 2.70; carapace

1.46 long, 1.00 wide; tibia+patella I 1.16. *Colour:* carapace, chelicerae and sternum uniform orange brown; legs yellowish brown with patellae and extremities of femora and tibiae paler; abdomen: dorsum dark sepia with five white spots: one spot on either side adjacent with a narrow, pale yellow scutum, one pair in the middle and a single spot in front of the spinnerets; sides dark with two oblique stripes near the back; venter pale yellow in front of epigastric fold, pale behind it with two broad, sinuous longitudinal dark bands. Carapace and sternum with fairly coarse reticulations. *Eyes* (measurements in mm): a, 0.05; b, 0.07; c, 0.07; d, 0.08; e, 0.02; f, 0.02; g, 0.04; h, 0.08; AL–AL, 0.13. MOQ:AW = 0.66 PW; AW = 0.54 L. *Clypeus* = 0.28 mm or 4.0 times diameter of ALE; chilum double, each part 0.08 high, 0.12 wide. *Leg spination:*

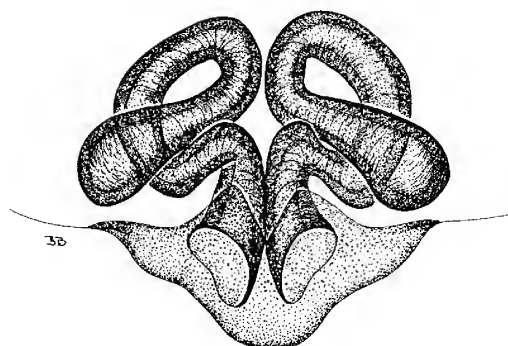
	F	P	T	Mt
I	d1	–	–	–
II	d1	–	–	v1
III	d1	pl1	pl1d2*v1	3 disp dw4
IV	d2*	pl1rl1	pl2*d2*rl2*v3*	5 disp dw5

Hinged hairs: TI d1, TII d1. *Male palp* (Figs. 21, 22): tibia with dorsolateral concavity, delimited by two retrolateral apophyses of which the ventrolateral one is very large; this explains why the concavity is rather dorsal than lateral;

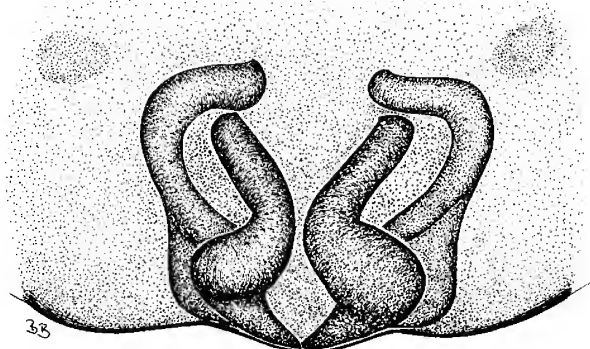
37



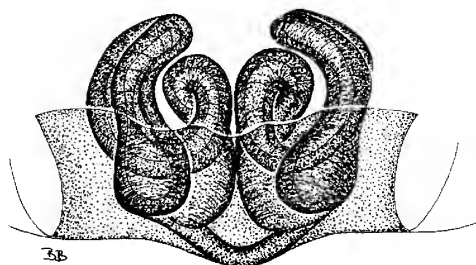
38



39



40



Figures 37–40. Epigynes, ventral view (left), dorsal view of cleared epigyne (right); 37–38, *A. biperforatum* n.sp.; 39–40, *A. grayi* n.sp. Scale = 0.1 mm.

ventrolateral apophysis with large dorsal part provided with a short sharp tip pointing down and large ventral prong pointing forward, rounded and swollen at extremity, produced under proximal part of cymbial flange; dorsal apophysis a broad transverse ridge with a prolateral macroseta; cymbium with flat flange; embolus fairly long and twisted with large, triangular basal apophysis, with strongly concave prolateral side; VTA massive and complex, its base with sharp retrolateral prong convergent with well-developed LTA; DTA membranous, with very narrow base suddenly widened into large rounded main part.

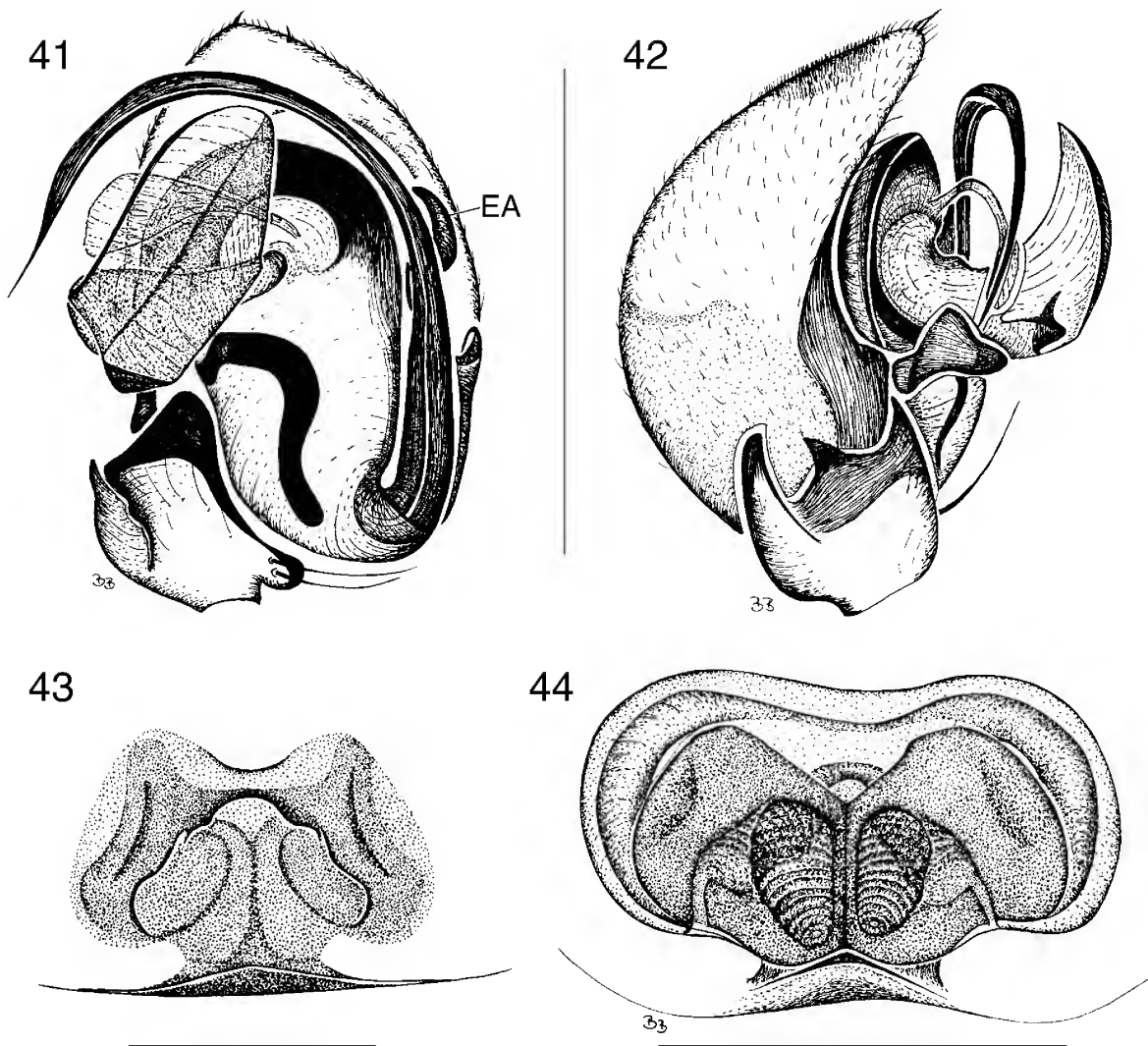
Female: total length 3.56; carapace 1.56 long, 1.02 wide; tibia+patella I 1.02. **Colour:** carapace, chelicerae and sternum uniform orange brown; legs yellowish brown with patellae and extremities of femora and tibiae paler; abdomen: dorsum dark sepia with five white spots: one pair in front, one pair in the middle and a single spot in front of the spinnerets; sides dark mottled with white, spots forming two faint oblique pale stripes near spinnerets; venter pale with broad dark central band, itself with pale, poorly delimited

spot in centre. Carapace on side with fairly coarse reticulations; sternum finely reticulated. **Eyes** (measurements in mm): a, 0.07; b, 0.10; c, 0.09; d, 0.10; e, 0.01; f, 0.03; g, 0.05; h, 0.09; AL–AL, 0.16. MOQ:AW = 0.50 PW; AW = 0.68 L. **Clypeus** = 0.28 mm or 2.8 times diameter of ALE; chilum double, each part 0.06 high, 0.22 wide. **Leg spination:**

	F	P	T	Mt
I	d1	–	–	–
II	d1	–	–	–
III	d1	–	pl2*d2*v1	4 disp dw5
IV	d1	–	pl2*d2*r12*v2*	5 disp dw5

Hinged hairs: TI d1, TII d1. **Epigyne** (Figs. 35, 36): poorly sclerotized oval area with wide depression in posterior half; epigynal opening small, central. Proximal part of copulatory ducts directed down- and forwards, thence towards the side and back towards the centre to end in poorly defined spermathecae after a final lateral loop.

Distribution. New South Wales (Fig. 45).



Figures 41–44. *Pseudasteron simile* n.gen., n.sp. 41, male palp, ventral view; 42, male palp, retrolateral view; 43, epigyne, ventral view; 44, epigyne cleared, dorsal view. Scales (mm) = 0.5 (41, 42), 0.25 (43, 44).

Etymology. The species name is a patronym in honour of one of the collectors of the type.

Asteron biperforatum n.sp.

Figs. 37, 38, 45

Type material. HOLOTYPE ♀: Australia, SE Queensland, Kenilworth SF, Sunday Creek, 9.8 km W of Charlie Moreland Park, 26°40'11"S 152°36'35"E, 6.v.1998, G. Milledge, wet sclerophyll forest (AM KS55637).

Other material. None.

Diagnosis. Females of this species are easily recognised by the paired epigynal openings whereas in the other females of the genus, the opening is single and most often hardly visible since it is often slit-shaped.

Description. *Female* (holotype): total length 3.10; carapace 1.52 long, 1.06 wide; tibia+patella I 1.12. *Colour:* carapace,

chelicerae and sternum uniform orange brown; legs yellowish brown with patellae and extremities of femora and tibiae paler; abdomen: dorsum dark sepia with five white spots: one pair in front, one pair in the middle and a single spot in front of the spinnerets; sides with two large pale spots, leaving an oblique dark stripe and some dark in front of the spinnerets; venter dark with a large rectangular spot behind the epigastric fold and a yellow sclerotized patch in front of the tracheal spiracle. Carapace on side with fairly coarse reticulations; sternum finely reticulated. *Eyes* (measurements in mm): a, 0.07; b, 0.08; c, 0.08; d, 0.09; e, 0.02; f, 0.05; g, 0.05; h, 0.09; AL–AL, 0.13. MOQ:AW = 0.70 PW; AW = 0.54 L. *Clypeus* = 0.30 mm or 3.7 times diameter of ALE; chilum double, each part 0.10 high, 0.20 wide. *Leg spination:*

	F	P	T	Mt
I	d1	–	–	–
II	d1	–	–	v1
III	d1	pl1rl1	pl2*d2*r1lv1	3 disp dw5
IV	d2*	pl1rl1	pl2*d2*r12*v3*	6 disp dw5

Hinged hairs: TI d1, TII d1. *Epigyne* (Figs. 37, 38): poorly sclerotized oval area with strongly protruding posterior rim; provided with paired epigynal openings. Proximal part of copulatory ducts funnel-shaped, strongly curved outwards and forwards, thence backwards, ending in poorly delimited spermathecae.

Male unknown.

Distribution. Known only from type locality (Fig. 45).

Etymology. The species name is an adjective referring to the openings of the epigyne.

Asteron grayi n.sp.

Figs. 23, 24, 39, 40, 45

Type material. HOLOTYPE ♂: New South Wales, Mummel Forest Rd, 8.8 km N of junction with Enfield Forest Rd, 31°16'S 151°50'E, Enfield SF, 163AS, 1350 m, 4.ii–9.iv.1993, M. Gray & G. Cassis (AM KS039147). PARATYPES: NEW SOUTH WALES: 1♂, 14♀ ♀, together with holotype (2♀ ♀ in ZSM, 2♀ ♀ in KBIN); 1♂, Bulls Ground SF nr Wauchope, 31°33'S 152°38'E, 10.ii.1991, NSW Forestry, A. York, (AM KS043360); 1♀, as previous (AM KS43369); 2♀ ♀, as previous (AM KS43367); 3♂ ♂, as previous (AM KS43362); 1♂, as previous (AM KS43358); 1♂, as previous (AM KS43359); 1♀, as previous (AM KS43366); 2♀ ♀, as previous (AM KS43364); 2♀ ♀, as previous (AM KS43370); 1♂, as previous (AM KS43357); 1♀, as previous (AM KS43365); 2♀ ♀, as previous (AM KS43368); 1♀, as previous (AM KS043371); 1♂, as previous (AM KS043356); 1♂, Bulls Ground SF, nr Wauchope, 10.ii.1995, A. York (AM KS43361); 1♂, 6♀ ♀, Barrington Tops SF, Tugalow Ck, Barrington Trail (E side of trail), 31°54'S 151°26'E, 4.ii–9.iv.1993, 1370 m, M. Gray & G. Cassis (62CG) (AM KS039174); 2♀ ♀, 1.3 km S along Bungaree Trail from Barrington Tops Forest Road, 31°56'S 151°21'E, SF 1180 m, 4.ii–9.iv.1993, M. Gray & G. Cassis (KS039173); 1♂, 1.9 km W along Sheas Nob Rd from Boundary CK Rd, 29°59'S 152°34'E, Boundary Creek State Forest 550, 4.ii–9.iv.1993, M. Gray & G. Cassis, (KS039043); 1♀, 1 km E of main road, 28°49'S 152°11'E, Boorook SF, 163A 900, 4.ii–9.iv.1993, M. Gray & G. Cassis, (AM KS036310); 1♂, 0.4 km S along Barrington Trail from southern Green Gap turnoff, 31°56'S 151°26'E, Stewarts Brook SF, 1460 m (NPWS Survey), 4.ii–9.iv.1993, M. Gray & G. Cassis, (KS039042); 5♀ ♀, Double Dumps Fire trail, 700 m off Daisy Patch Rd, 31°20'S 151°54'E, Enfield SF, 1080 m, 4.ii–9.iv.1993, M. Gray & G. Cassis (KS039148); 1♂, 1♀, 0.25 km S of junction Turbrabucca & Omadale Brook Roads, 31°54'S 151°23'E, Stewart SF, 1290 m, NPWS Survey, 4.ii–9.iv.1993, M. Gray & G. Cassis (KS039172); 1♀, NE facing slope above Kunderang Station Ck, 30°48'S 152°06'E, 410 m, NPWS Survey, 4.ii–9.iv.1993, M. Gray & G. Cassis (KS039150); 1♀, 45BM Farnell Fire Trail, ca. 1.2 km N of junction with Upper Rocky River, Fire Trail, 29°20'S 152°09'E, Spirabo SF, 1110 m, 4.ii–9.iv.1993, M. Gray & G. Cassis (KS036287); 1♀, North West Fire Trail, 29°27'S 152°16'E, Washpool NP, 950 m, 4.ii–9.iv.1993, M. Gray & G. Cassis (KS036421); 1♀, Daisy Patch Fire Trail, 1.9 km S of Enfield Rd, 31°20'S 151°54'E, Enfield SF, 1130 m, 4.ii–9.iv.1993, M. Gray & G. Cassis (AM KS039175); 6♀ ♀, W of junction Thunderbolts Track & Devils Hole Track, 31°54'S 151°28'E, Barrington Tops SF, 1420 m, 4.ii–9.iv.1993, M. Gray & G. Cassis, (KS039176); 1♀, 0.7 km W. along unnamed logging track from Omadale Brook Rd, 31°54'S 151°23'E, Stewarts Brook SF, 1250 m, NPWS Survey, 4.ii–9.iv.1993, M. Gray & G. Cassis (AM KS039485); 1♂, Bulls Ground SF, nr Wauchope, 10.ii.1991, A. York, M. Gray (AM KS043363); 1♀, Booti Booti NP, 13.vii.1996, L. Wilkie & R. Harris (AM KS50446); 1♀, Slave Cave, Doline via Wellarawong, 33°24'S 150°00'E, 20.v.1994, J. Moss & G.S. Hunt (AM KS45492); 1♀, Dodds Fire Trail, 1 km from Enfield Rd, 31°23'S 151°53'E, Enfield Sate Forest, 1050 m,

4.ii–9.iv.1993, M. Gray & G. Cassis (AM KS039149); 1♀, Belowra Rd, Dampier SF, 36°09'28"S 149°50'20"E, 10.iii.1999, J. Tarnawski, S. Lassau (AM KS55902); 1♀, Turtle Creek Fire Trail, Monga SF, 35°38'20"S 149°55'51"E, 15.iii.1999, L. Wilkie, R. Harris, H. Smith (AM KS55903).

Other material. None.

Diagnosis. Males of this species are recognised by the shape of the dorsolateral tibial apophysis which is large and ear-shaped, appearing as spine-shaped with parallel margins in lateral view, and by the LTA which has a straight, sharp tip, pointing outwards in ventral view. Females may be recognised by the epigyne provided with a diamond-shaped, pale central area just in front of posterior margin.

Description. *Male* (holotype): total length 2.82; carapace 1.38 long, 0.94 wide; tibia+patella I 1.06. *Colour:* carapace and chelicerae uniform medium; sternum reddish brown; legs uniform yellowish brown; abdominal pattern: dorsum dark sepia with five white spots: one spot on either side adjacent with a narrow, brownish scutum, one pair in the middle and a single spot in front of the spinnerets; sides dark with several oblique pale stripes; venter with two large lateral and one smaller central pale spots behind epigastric fold and yellowish area, covering tracheal spiracle. Carapace and sternum with fairly coarse reticulations. *Eyes* (measurements in mm): a, 0.06; b, 0.06; c, 0.07; d, 0.08; e, 0.02; f, 0.03; g, 0.04; h, 0.08; AL–AL, 0.14. MOQ:AW = 0.77 PW; AW = 0.70 L. *Leg spination:*

	F	P	T	Mt
I	d1	–	–	–
II	d1	–	–	v1
III	d1	pl1rl1	pl2*d2*v1	3 disp dw5
IV	d2*	pl1rl1	pl2*d2*rl2*v2*	5 disp dw5

Hinged hairs: TI d1, TII d1. *Male palp* (Figs. 23, 24): tibia with very shallow retrolateral concavity, delimited by two apophyses: ventrolateral apophysis pointing forward, blunt, produced under proximal part of cymbial flange, dorso-lateral one large, ear-shaped as seen from in front, appearing as parallel-shaped spine in lateral view; cymbium with flat flange, its inferior margin clearly concave; embolus and VTA as in other species; LTA short, appearing as short, straight spine in ventral view; DTA membranous, roughly triangular: strongly widened from narrow base.

Female (paratype): total length 2.92; carapace 1.36 long, 0.96 wide; tibia+patella I 0.98. *Colour:* as in male except for absence of dorsal abdominal scutum and pale central spot behind epigastric fold, smaller thus forming a continuous central dark band provided with a series of small pale spots. Carapace and sternum reticulated. *Eyes* (measurements in mm): a, 0.06; b, 0.06; c, 0.07; d, 0.08; e, 0.02; f, 0.03; g, 0.04; h, 0.08; AL–AL, 0.15. MOQ:AW = 0.77 PW; AW = 0.70 L. *Leg spination* and *hinged hairs* exactly as in male. *Epigyne* (Figs. 39, 40): a poorly sclerotized oval area with dark curved copulatory ducts clearly visible under cuticle leaving a diamond-shaped pale area just in front of posterior margin.

Variation. Colour pattern fairly stable, but venter variable in the amount of white; spination stable; male carapace length and width vary between 1.34 and 1.44, 0.93 and 0.97;

female carapace between 1.32 and 1.41, 0.93 and 0.99.

Distribution. Known only from New South Wales (Fig. 45).

Etymology. The species name is a patronym in honour of the collector of the type.

Pseudasteron n.gen.

Diagnosis. The genus is closely related and similar to *Asteron*; the main differences of *Pseudasteron* are that it has: AME touching, chilum single, carapace entirely reticulated, abdominal scutum fairly large in males. Some male palpal characters are also diagnostic: ventrolateral tibial apophysis bifid; embolus ribbon-shaped and with fairly large, curved apophysis.

Description. Small spiders (2.50–3.00) with reticulated tegument. Carapace entirely reticulated (Fig. 9) at its widest between coxae II and III, narrowed to 0.65 maximum width in females, to about 0.55 maximum width in males. Profile domed with highest point between fovea and PME. *Colour:* carapace, chelicerae and sternum medium brown; legs orange; abdomen dark grey with five pale spots; in male provided with dark sepia, fairly wide scutum in anterior half. Eyes in two strongly procurved rows, resulting in (2–4–2) situation, PLE situated level with PME. All eyes subequal, circular, and pale, only AME dark. AME touching and about less than half the radius from PME which are slightly larger. ALE twice their diameter apart. MOQ longer than wide and narrower in front than at the back. Clypeus slightly convex and retreating; about 3 times the diameter of an ALE; with few hairs. Chilum a single triangular sclerite, slightly wider than long, without hairs. Chelicerae with a few hairs in front and a dense row on distal promargin; no teeth. Labium narrowed at base; sparsely haired. Gnathocoxae rather elongate; sparsely haired; with anteromesal scopula. Sternum fairly flat, triangular with straight anterior margin and slight triangular extensions between coxae. No inter- nor precoxal sclerites. *Legs:* formula 4 1 2 3. Spination: few spines on pairs I and II, more numerous on III and IV. Tarsal claws with approximately 14 teeth on those of first leg pairs, with only about 7 teeth on those of legs III and IV. Single claw on very small onychium. Trichobothria in two rows on T and in a single row on Mt and t. No hinged hairs in male, only on TI and II in female. Metatarsal preening brush poorly developed, composed of chisel-shaped hairs. *Abdomen:* oval; with two sigilla; in the male with fairly large dorsal scutum in anterior half and with poorly developed epiandrium. Tracheal spiracle narrow without sclerotized area in front. Spinnerets as usual in the family; posterior pairs smaller in males than in females. Colulus represented by few hairs. *Male palp:* tibia with a frontolateral concavity delimited by dorsolateral and ventrolateral apophyses; dorsal one usually flat, ventral one strong, bifid, embracing cymbial flange. Embolus long, ribbon-shaped with large, folded, retrolateral apophysis at base, VTA large, flat; DTA membranous, fan-shaped; LTA short. *Epigyne:* poorly sclerotized showing strong copulatory ducts under cuticle; epigynal openings rounded and slit-shaped; copulatory ducts with fairly constant trajectory, leading to widely separated, poorly delimited spermathecae. *Female palp* with slender,

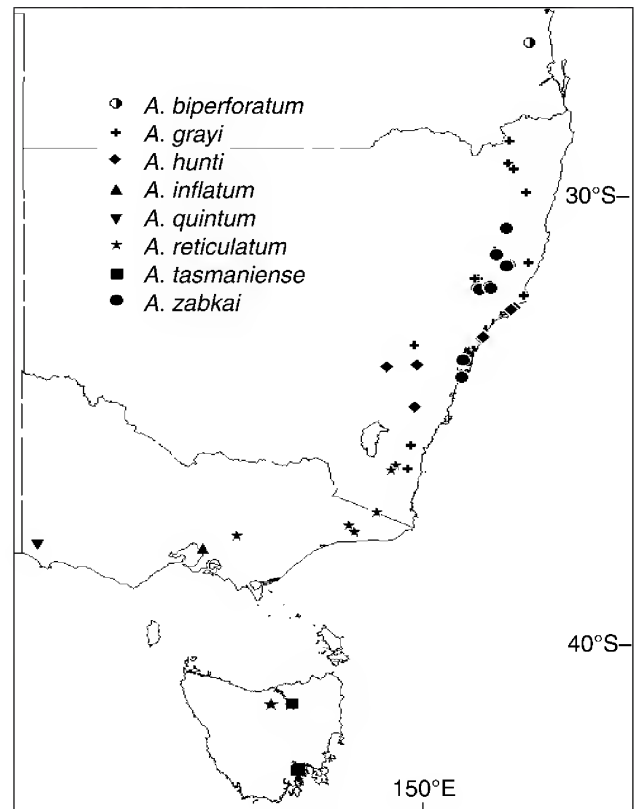


Figure 45. Southeastern Australia showing collecting localities of *Asteron* species.

conical tarsus with spines on prolateral and ventral sides. Finely dentate tarsal claw turned inward over $\pm 30^\circ$.

Distribution. Queensland.

Type species. *Pseudasteron simile* n.sp.

Pseudasteron simile n.sp.

Figs. 3, 4, 9–12, 14, 41–44, 46

Type material. HOLOTYPE δ : SE Queensland: Braemar SF, 15–19.x.1979 27°13'S 150°50'E, litter funnel extraction, R. Raven (QM S3854). PARATYPES: QUEENSLAND: 3 ϕ ϕ , SE Qld, together with holotype; 3 δ δ , 7 ϕ ϕ , Lake Broadwater, via Dalby, pitfall site 8, 17.v–24.xi.1985, QM & M. Bennie (QM S15734; 1 δ , 1 ϕ in ZSM); 1 δ , 2 ϕ ϕ , Braemar SF, 27°13'S 150°50'E, 18.x.1979, open woodland, sifted litter, G. Monteith (QM S4282); 3 ϕ ϕ , Braemar SF, 4–8.ii.1980, R. Raven (QM S4246); NE Qld: 1 δ , Tooloombah Ck, 22°42'S 149°34'E, 29.vii–24.xi.1992, pitfalls, R. Raven, P. & E. Lawless, M. Shaw (QM S24518); 1 δ , as previous (QM S24502); 1 ϕ , Tooloombah Ck, 22°42'30"S 149°34'E, 29.vii–24.xi.1992, dry *Acacia/Eucalyptus* woodland, QM Pitfall NQ41, Raven, Lawless & Shaw (QM S24638); 1 ϕ , SE Qld, Expedition Ra NP, "Amphitheatre" camp, 25°12'S 148°59'E, 18.xii.1997–5.iii.1998, 560 m, open forest pitfall, Cook & Monteith (QM S33364); 2 δ δ , SE Qld, Hamphery Racetrack, 25°38'S 151°30'E, 11.x–18.xii.1998, 140 m, pitfall 7519, Monteith & Gough (QM S47509); 1 ϕ , central Qld, Moranbah, 5 km S, 240 m, 22°02'S 148°03'E, 20.xii.1997–26.iv.1998, pitfall trap 5798, Bendee Scrub, G.B. Monteith (QM S47510); 2 ϕ ϕ , SE Qld, Binjour, Redvale Rd, 340 m, 25°33'S 151°28'E, 20.xii.1997–26.iv.1998, open forest, flight intercept, 5795, G.B. Monteith (QM S47511); 1 δ , NE Qld, Moranbah, 5 km S, 22°02'S 148°03'E, 25.vi–20.xii.1997, intercept, Bendee Scrub,

5642, Monteith & Kruck (QM S47512); 1 ♀, NE Qld, Davies Creek NP, 17°00'S 145°34'E, 29.x.1991–23.vii.1992, pitfall NQ8, P. Lawless, R. Raven & Shaw (QM S22705); 2 ♂♂, 5 ♀♀, as previous (QM S22730); 2 ♂♂, 2 ♀♀, as previous (QM S25149); 11 ♂♂, 19 ♀♀, as previous but collected 26.xi.1992–15.iv.1993 (QM S19782; 2 ♂♂, 2 ♀♀ in ZSM; 2 ♂♂, 2 ♀♀ in KBIN).

Other material. None.

Diagnosis. The species is recognised by the uniform colour and the poorly spined legs; the male is characterised by the large dorsal embolar apophysis; the female by the transverse, curved plate in the anterior part of the epigyne, in front of the shallow central depression connecting the openings.

Description. *Male* (holotype): total length 2.60; carapace 1.35 long, 0.93 wide; tibia+patella I 0.96. *Colour:* carapace, chelicerae and sternum uniform orange. Legs pale yellow. Abdomen: dark sepia with some pale mottling. Dorsum with fairly large scutum in anterior half; 5 pale spots, the second pair merging with pale lateral sides; these provided with three oblique stripes in posterior half. Venter pale with four dark spots: two just behind epigyne, two in the middle. Carapace finely granulated; sternum not granulated. *Eyes* (measurements in mm): a, 0.06; b, 0.08; c, 0.07; d, 0.06; e, 0.00; f, 0.02; g, 0.04; h, 0.08; AL–AL, 0.12. MOQ:AW = 0.66 PW; AW = 0.60 L. Chilum single, 0.11 wide, 0.07 high. *Leg spination:*

	F	P	T	Mt
I	d1	–	–	–
II	d1	–	–	–
III	–	pl1	pl1d2v1	dw4
IV	d2	pl1rl1	pl2d2rl2v1–1	4 disp dw5

No hinged hairs. Metatarsi I and II fusiform. *Male palp* (Figs. 41, 42): tibia with two retrolateral apophyses delimiting concavity; dorsal apophysis complex well developed, blunt; ventrolateral one broad with concave anterior edge, sharp dorsal tip, ventral part folded around cymbial flange. Cymbium short with well-developed short flange. Embolus originating on posterior rim of tegulum; proximal part straight and directed forwards, distal part semicircular; long embolar apophysis with distal part twisted and wrapped around embolus. VTA large, foliate, sclerotized but translucent. DTA narrow and membranous.

Female (paratype): total length 2.86; carapace 1.35 long, 0.96 wide; tibia+patella I: 0.88. *Colour:* exactly as in male. *Eyes:* exactly as in male. Chilum single, 0.12 wide, 0.08 high. *Leg spination:*

	F	P	T	Mt
I	d1	–	–	–
II	d1	–	–	–
III	–	pl1	pl1d2rl1v1	dw5
IV	d2	pl1rl1	pl2d2rl2v1–1	4 disp dw5

No hinged hairs. Tarsi I and II cylindrical. *Epigyne* (Figs. 14, 43, 44): with frontal margin anterior to epigynal openings and slightly convex. Spermathecae close together.

Variation. Colour pattern and size stable; male carapace length and width vary between 1.27 and 1.35, and 0.91 and 0.94; female carapace between 1.22 and 1.38, 0.83 and 0.96.

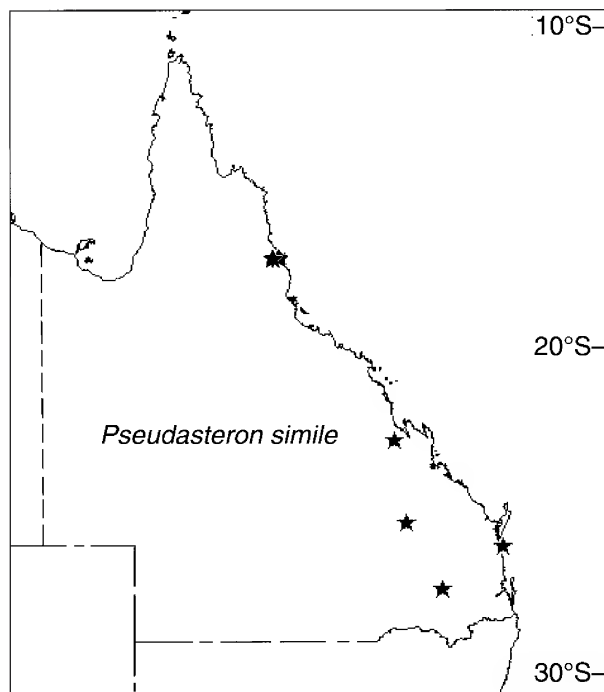


Figure 46. Queensland, showing collection localities of *Pseudasteron simile*.

Distribution. Known from southern and central Queensland (Fig. 46).

Etymology. The name refers to the superficial similarity (Latin: *similis* = similar) of the species with the type species of *Asteron* to which this species was originally thought to belong.

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Systematics of the *Litoria citropa* (Anura: Hylidae) Complex in Northern New South Wales and Southern Queensland, Australia, With the Description of a New Species

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ABSTRACT. We describe a new hylid frog, *Litoria daviesae* n.sp., from the highlands of mid-eastern New South Wales, Australia. The new species was formerly included in *L. subglandulosa*, from which it is now distinguished by allozyme and mitochondrial DNA profiles, colour and adult size. The geographic ranges of both species include several widely spaced conservation reserves. The conservation status of *L. subglandulosa* requires further investigation in the light of recent reported declines. *Litoria daviesae* n.sp. occurs in a series of apparently disjunct populations above 400 m altitude along the eastern escarpment and adjacent tablelands of the Great Dividing Range. The larvae of *L. daviesae* n.sp. occur in permanent streams and the adults are closely associated with the riparian zone.

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The forests of the coast and Great Dividing Range of eastern Australia contain a number of endemic hylid frog radiations. One of these, the *Litoria citropa* species group (Tyler & Davies, 1978, 1985), presently comprises a number of smaller leaf green coloured species and two larger species, *L. citropa* and *L. subglandulosa* both with prominent submandibular glands. Except for a nomenclatural issue concerning the usage of a species epithet (Tyler & Anstis,

1983), the systematics of the two larger species has been stable since *L. subglandulosa* was described by Tyler & Anstis (1975). The reproductive and larval biology and distributions of the species are well described (Anstis & Littlejohn, 1996).

Several species of frogs from eastern Australia have either disappeared or have suffered notable declines in their abundance and range (Ingram & McDonald, 1993; Richards

et al., 1993; Mahony, 1996). In particular, two species of hylids, *Litoria castanea* and *L. piperata*, originally found within the range of *L. subglandulosa*, have disappeared while *L. subglandulosa* has undergone a decline in abundance (Mahony, 1996). Historically, *L. subglandulosa* was known from a small number of locations, and its range has been revised recently to include the northern catchment of the Hunter River in central New South Wales (Anstis & Littlejohn, 1996).

Litoria subglandulosa was listed as vulnerable in the New South Wales Threatened Species Conservation Act, 1995, because it was considered to be a habitat specialist, with a restricted distribution and Lunney *et al.* (1996a,b) presented evidence of population declines. The species has never been considered to be common (Tyler & Anstis, 1975; Anstis & Littlejohn, 1996; Anstis, 1997). Recent comprehensive surveys show that it has declined in abundance from particular geographic regions (NSW NPWS 1994; Anstis, 1997).

Recent molecular and morphological analyses of the species groups of hylid frogs from eastern Australia have identified the presence of additional and in some cases "cryptic" species (Donnellan *et al.*, 1999). As part of the assessment of the conservation status of *Litoria subglandulosa*, we undertook a molecular and morphological analysis to assess whether the species harboured any cryptic taxa. The presence of undetected taxa within what is thought to be single taxon that is under investigation for conservation and management can potentially lead to mismanagement of the conservation of biodiversity (Parnaby, 1991; Donnellan *et al.*, 1993). We have also made an assessment of the conservation status of populations based on specimen records from museum collections, biological survey data, and the field notes of individual workers.

Materials and methods

Material examined. Specimens examined are listed in the Appendix. Institutional abbreviations follow Leviton *et al.* (1985). We used a number of other species of *Litoria* as outgroups or for other comparative purposes. We included taxa from the *L. phyllochroa* species complex, which appears to comprise more species than are presently recognized (Donnellan *et al.*, 1999). These are labelled *L. nudidigitus*, *L. phyllochroa*, *L. pearsoniana*-1 and *L. pearsoniana*-2.

Allozyme electrophoresis. Frozen tissues were available from 24 specimens of *Litoria* from nine localities in northern New South Wales (Appendix, Fig. 1). These included *L. citropa*, *L. pearsoniana*-2 and *L. spenceri* to allow an assessment of evolutionary relationships among the taxa of the *L. citropa* species group and to help identify misidentified specimens that might be present in the sample. Allozyme electrophoresis of liver homogenates was performed on Cellologel (Chemetron, Milan) according to the methods of Richardson *et al.* (1986). The enzyme products of 32 presumptive loci were scored. The enzymes (and proteins) stained and Enzyme Commission numbers were: aspartate aminotransferase (AAT, EC 2.6.1.1), aconitate hydratase (ACOH, EC 4.2.1.3), aminoacylase (ACYC, EC 3.5.1.14), adenylate kinase (AK, EC 2.7.4.3),

dihydrolipoamide dehydrogenase (DDH, EC 1.8.1.4), enolase (ENO, EC 4.2.1.11), fructose-bisphosphatase (FBP, EC 3.1.3.11), fumarate hydratase (FUMH, EC 4.2.1.2), glycerol-3-phosphate dehydrogenase (G3PDH, EC 1.1.1.8), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), glutamate dehydrogenase (GTDH, EC 1.4.1.3), 3-hydroxybutyrate dehydrogenase (HBDH, EC 1.1.1.30), isocitrate dehydrogenase (IDH, EC 1.1.1.42), cytosol aminopeptidase (LAP, EC 3.4.11.1), L-lactate dehydrogenase (LDH, EC 1.1.1.27), lactoylglutathione lyase (LGL, EC 4.4.1.5), malate dehydrogenase (MDH, EC 1.1.1.37), mannose-6-phosphate isomerase (MPI, EC 5.3.1.8), nucleoside-diphosphate kinase (NDPK, EC 2.7.4.6), dipeptidase (PEP-A, EC 3.4.13.?), tripeptide aminopeptidase (PEP-B, EC 3.4.11.?), proline dipeptidase (PEP-D, EC 3.4.13.?), phosphoglycerate mutase (PGAM, EC 5.4.2.1), phosphogluconate dehydrogenase (PGDH, EC 1.1.1.44), phosphoglycerate kinase (PGK, EC 2.7.2.3), phosphoglucomutase (PGM, EC 5.4.2.2), and triose-phosphate isomerase (TPI, EC 5.3.1.1). Alleles were identified by comparison with samples that were repeatedly included on each gel (internal controls) and through critical side-by-side comparisons (line-ups; see Richardson *et al.*, 1986). To facilitate the analysis of data, specimens of a single genetic type from a single location (i.e., where there were no fixed differences [Richardson *et al.*, 1986]), were treated as an Operational Taxonomic Unit (OTU) (Tables 1 and 2, Fig. 1). Evolutionary relationships among the OTUs were recovered by conducting heuristic searches under the maximum parsimony criterion of optimality (MP) implemented in PAUP* 4.0b3 (Swofford, 1999). Loci were treated as characters, alleles as unordered character states and polymorphisms as uncertainties. Robustness of phylogenetic hypotheses was estimated from bootstrap proportions among 10,000 pseudoreplicates with the "fast" heuristic search option in PAUP* 4.0b3. A genetic distance analysis was based on Cavalli-Sforza chord distances between OTUs (Cavalli-Sforza & Edwards, 1967) generated with BIOSYS-1 (Swofford & Selander, 1981) using the tree-building Neighbor Joining (NJ) algorithm implemented with the NEIGHBOR routine in PHYLIP Version 3.5 (Felsenstein, 1993).

Mitochondrial DNA. See the Appendix for details of specimens examined. Liver samples were kept frozen at -70°C until used for DNA extraction. Total cellular DNA was extracted with the salting out procedure of Miller *et al.* (1988) and stored at -20°C. For polymerase chain reaction (PCR) amplifications, 50–100ng of DNA was added to a 50µl reaction mixture containing 4mM MgCl₂, 1X reaction buffer, 0.8mM dNTPs 0.4mM primers, 1 unit of Biotech *Tth* plus DNA polymerase and the remaining volume of dH₂O. Reaction mixtures were overlaid with 60–90µl of mineral oil. The primers used for 16S rRNA amplification (16sar and 16sbr) were designed by Cunningham *et al.* (1992), and for ND4 (Limno2 and ND4) were designed by C. Schauble, University of Queensland and Arévalo *et al.* (1994) respectively. Amplification was carried out on a Corbett FTS-320 Thermal Sequencer and comprised a single cycle of denaturation for 3 min at 94°C, annealing for 45 s at 55°C and extension for 1 min at 72°C, followed by 29

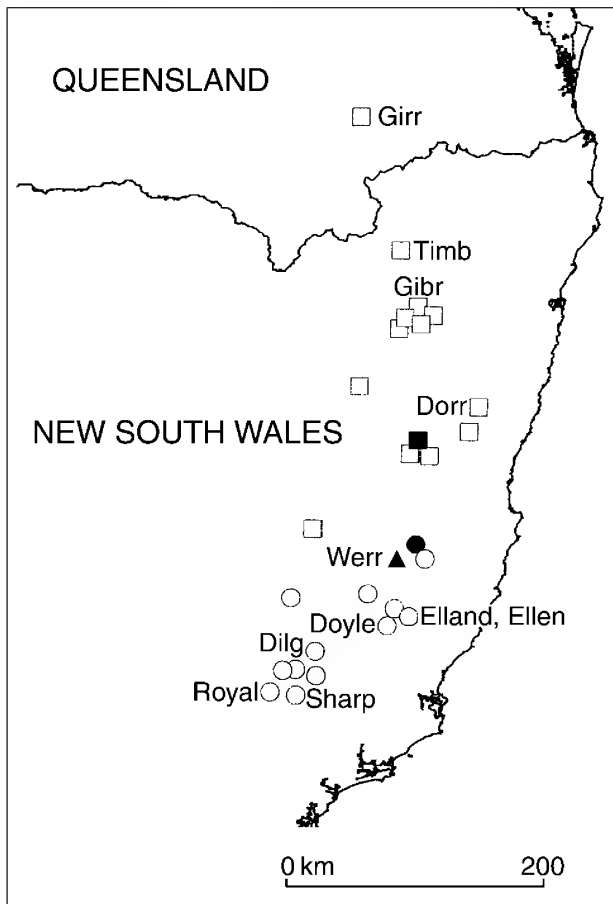


Figure 1. Map of eastern Australia showing collection locations for specimens of *Litoria* examined. Abbreviations refer to site locations where specimens were examined by molecular methods (see Appendix for key to codes). *Litoria subglandulosa* (□), *L. daviesae* (○), specimens of undetermined species (●), and type localities of *L. daviesae* (▲) and *L. subglandulosa* (■).

cycles of 94°C for 45 s, 55°C for 45 s and 72°C for 1 min, ending with a single extension step of 72°C for 6 min. PCR products were purified for sequencing using a Bresa-Clean DNA Purification Kit (Bresatec), following the manufacturer's protocol for DNA extraction from solutions.

Each sample had both strands sequenced directly from the PCR product using the original PCR primers. Products were cycle-sequenced on a Corbett FTS-1 Thermal Sequencer using the Applied Biosystems PRISM Ready Reaction DyeDeoxy Terminator Cycle sequencing kit, following the manufacturer's instructions. The sequencing program consisted of 25 cycles of 94°C for 30 s, 50°C for 15 s and 60°C for 4 min. Cycle-sequenced product was electrophoresed and viewed on an Applied Biosystems Model 373A Sequencing System.

Partial sequences of 16S *rRNA* from *L. nudidigitus*, *L. phyllochroa*, *L. pearsoniana*-1 and -2, and *L. spenceri* were obtained from Donnellan *et al.* (1999) and are available from the European Bioinformatics Institute Server: <http://ftp.embl-heidelberg.de/pub/databases/embl/align/> (alignment ds38337). *Litoria caerulea* was used as an outgroup, as an ongoing study of relationships within the Australasian Hylidae shows this species to be a member of one of several species groups closely related to the *L. citropa* species group (Donnellan & Monis, unpubl. data). Sequences were aligned with CLUSTALW (Thompson *et al.*, 1994) and improved by eye without reference to secondary structure models as the alignment required the insertion of few gaps. GenBank accession numbers for these sequences are 16S *rRNA*: AF2822609–14, ND4: AF282598–608. Evolutionary trees, constructed with the maximum parsimony (MP) or maximum likelihood (ML) criteria of optimality, were found with heuristic searches implemented in PAUP* 4.0b3 (Swofford, 1999). The robustness of phylogenetic hypotheses was tested with bootstrapping.

Morphological analysis. Measurements were taken with vernier callipers to the nearest 0.5 mm from formalin-fixed, alcohol-preserved specimens after the method of Tyler (1968). Measurements taken were: snout-vent length (SV), head length (HL), head width (HW), eye to naris distance (EN), internarial span (IN), eye length (E), greatest length of tympanum (T), eye to tympanum (ET), interocular span (IO), arm length (A), longest finger (4th) length (F), tibia length (TL), and longest toe (4th) length (P). T and ET were measured under a dissecting microscope. Sex was determined by the presence or absence of a nuptial pad in adults or by examination of gonad morphology after dissection.

Discriminant function analysis (DFA) was performed on log-transformed measurement data. Only individual specimens that had been given an *a priori* group classification based either on their genotype (allozyme profile or mitochondrial haplotype) or distribution (see below) were used to derive the DFA equation. All other measured specimens were then ascribed to one of the known OTUs using the DFA. Statistical analyses were conducted with the program Statistica release 5.1, 1997 edition (StatSoft, 1997).

Assessment of historical and current distribution.

Distributional records were obtained from the Australian (AMS), Queensland (QM) and South Australian (SAMA) museums, literature, and extensive field surveys in northeastern New South Wales conducted over the past seven years. Targeted systematic searches were conducted where suitable habitat occurred. Stream transects were conducted by day and night for a distance of 500 m. At the middle and ends of a transect, a sequence of male calls was broadcast for five minutes, at a level slightly greater than that normally produced by males, to elicit response from any males that may be present but not calling.

Results

Allozyme electrophoresis. Allele frequencies at the 32 loci resolved among the 12 OTUs are presented in Table 1. These data were converted into a matrix of percentage fixed allelic differences among the OTUs. A strict consensus tree summarising the 176 trees of length 35 steps found with MP is presented in Fig. 2a. Two lineages are apparent among the 8 OTUs classified *a priori* as *L. subglandulosa*: group 1 includes OTUs: Dilg, Elands, Ellen, Royal, Werr, and Doyle; and group 2 includes OTUs: Dorr, Gibr, and Timb. The groups differ by fixed allelic differences at four loci: *Acoh-2*, *Acyc*, *Idh-1*, and *Mpi* (Table 1) and are genetically uniform within each group with no fixed differences between OTUs within group 2. An apparent fixed difference at *Aat-2* in group 1 is due most likely to the small sample size. Each group is genetically well differentiated (approximately 50% fixed allelic differences) from the other members of the *L. citropa* species group included and the monotypic *L. spenceri* species group. The phenotype of individual SAMA R51060, typed for the four diagnostic loci only, was *Acoh-2*^c, *Acyc*^b, *Idh-1*^{ac}, and *Mpi*^c. This specimen is assignable to group 1 on the genotypes at these markers. Groups 1 and 2 are defined by apomorphic character states, group 1 at *Acyc*^a and *Idh-1*^c and group 2 at *Mpi*^c. The *Acoh-2* locus was parsimony uninformative. In the NJ tree generated from the genetic distance analysis (not shown), groups 1 and 2 were also present.

Mitochondrial DNA. A total of 547 aligned sites from the 16S rRNA nucleotide sequences were available for analysis from the 27 individuals sequenced. A total of 461 sites were invariant, 86 were variable and 46 were parsimony informative, the variable sites are listed in Table 2. Eleven different haplotypes were observed. Two haplotypes differing by 1.1% sequence divergence were found in *Litoria citropa*, a single haplotype was found among the 13 group 1 individuals and two different haplotypes were observed among the six group 2 individuals (haplotype 1: SAMA R51052; haplotype 2: SAMA R39108, R51051, ABTC 68396–8). The percentage uncorrected sequence divergence between the two haplotypes observed within group 2 was 0.6% and between these and the group 1 haplotype ranged from 2.1–2.3%. Percentage uncorrected sequence divergence of the outgroup to the 10 ingroup sequences ranged from 4.4–11.1%.

To analyse the phylogenetic relationships among the 11 haplotypes found among the 16S rRNA sequences, a 645 bp portion of the *ND4* gene was sequenced for each haplotype and the sequences of both genes were combined into a single analysis. The Incongruence Length Difference test of Farris *et al.* (1994), implemented in PAUP* as the “partition homogeneity test”, indicated that the sequence partitions could be combined, $P = 0.71$. The *ND4* sequences contributed 262 variable sites and 188 parsimony informative sites. Ingroup uncorrected sequence divergences for the *ND4* sequences ranged from 1.4–21.7%. A single MP tree, length 694 steps, was found with an unweighted heuristic search (Fig. 2b). Three major lineages are apparent, *L. citropa/spenceri*, *L. nudidigitus* /

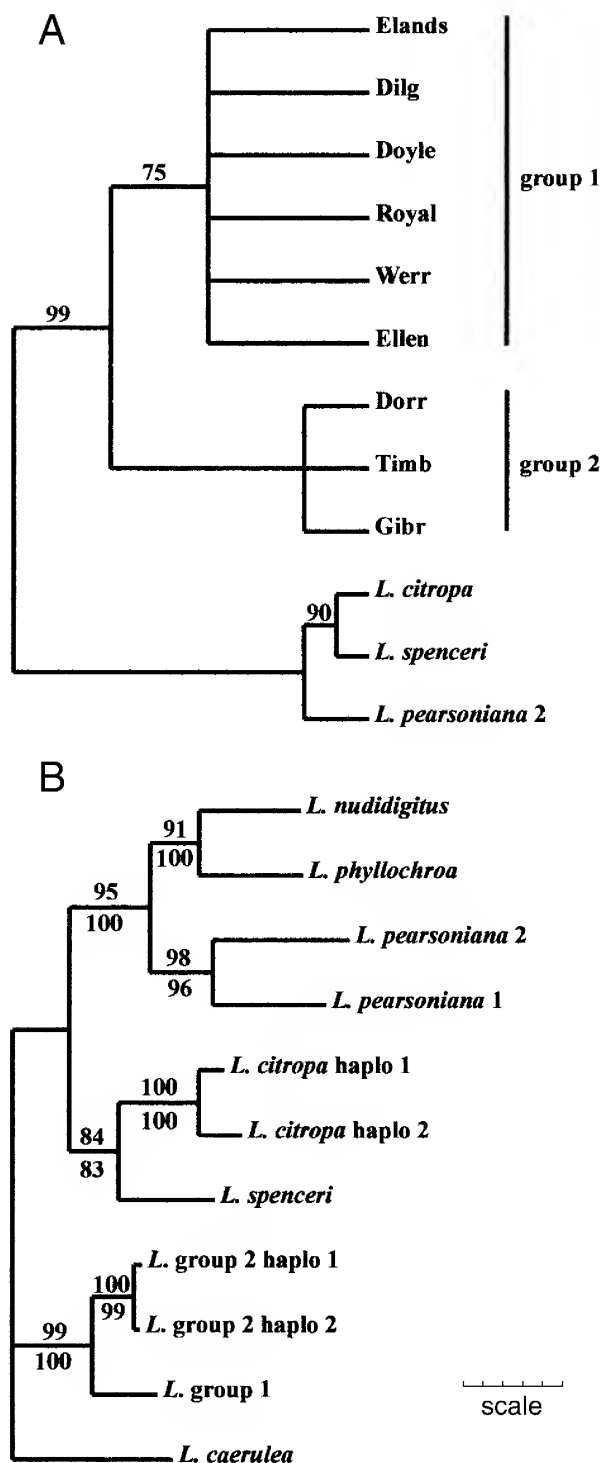


Figure 2. Evolutionary trees of *Litoria* based on (A) a strict consensus tree summarising the 176 equally most parsimonious trees based on the allozyme data. Bootstrap proportions are to the left of relevant nodes, and (B) a MP tree of relationships among concatenated mitochondrial 16S rRNA and ND4 nucleotide sequences. Values above and below the nodes represent bootstrap proportions greater than 50% among 2000 MP and 100 ML pseudoreplicates respectively. Scale bar represents 50 steps in MP analysis.

phyllochroa/pearsoniana-1 and -2, and group1/group2. The first two lineages form a sister group. The same three major lineages were present in the ML tree found with a heuristic search using the HKY85 model of sequence evolution (not shown). However the *nudidigitus/phyllochroa/pearsoniana*-1 and -2, and group1/group2 lineages form a sister group in the ML tree. Bootstrap proportions from 2000 MP and 100 ML pseudoreplicates (Fig. 2b) show strong support for each of the three major lineages, ie $\geq 80\%$, but support is absent for either of the sets of relationships among these lineages apparent in the MP or ML trees. All nodes within each of the three lineages receive strong support from both MP and ML bootstraps, ie $>95\%$. Of particular importance is the reciprocal monophyly of the group 1 and group 2 haplotypes, with very strong support from bootstrapping, ie 99–100%.

Morphological analysis. The *a priori* classified test base comprised specimens identified from either their genotype or on the basis of their distribution. For the non-genotyped sample, specimens from all locations south of $31^{\circ}14'S$ were included in group 1 while those from locations north of $30^{\circ}10'S$ were included group 2. These dividing lines were determined by allozyme electrophoresis. Specimens from locations between $30^{\circ}10'S$ and $31^{\circ}14'S$ were entered as *a priori* unclassified cases. Sample sizes were: group 1 ♂♂ $n = 19$; ♀♀ $n = 2$; group 2 ♂♂ $n = 13$; ♀♀ $n = 0$.

A standard DFA of males only, produced 100% *a posteriori* correct classification of group 1 individuals ($n = 19$) and 93% correct classification of group 2 individuals ($n = 13$), with a single individual (AMS R96910 from Gibraltar Range NP) misclassified. A forward stepwise DFA retained seven variables (A, T, IN, HL, ET, TL, E in decreasing order of significance) in the model but resulted in two individuals of group 2 being misclassified (AMS R96910 and SAMA R51052). [Standard Wilk's lambda = 0.203, approx. $F_{(13,19)} = 5.721$ $p < 0.000$; forward stepwise Wilk's lambda = 0.215, approx. $F_{(7,25)} = 13.068$ $p < 0.000$].

A standard DFA on the 13 variables with both sexes included produced 100% *a posteriori* correct classification of group 1 ($n = 21$) and 93% *a posteriori* correct classification of group 2 individuals ($n = 13$), with a single individual (AMS R96910 from Gibraltar Range NP) misclassified (Wilk's lambda 1.227 approximate $F_{(13,21)} = 5.510$ $p < 0.000$). In a forward stepwise DFA, eight variables in decreasing order of significance were used in the model: IN, T, TO, HL, ET, TL, FL and E.

In the DFA of *a priori* unclassified specimens from north of $31^{\circ}14'S$ and south of $30^{\circ}10'S$, 26 of the 27 males were classified as group 2. The single exception (SAMA R13506) was collected from a location with 24 other group 2 males.

Because the original test database did not include any group 2 females, we assigned females from locations where males were present to the same taxon as those males. In particular, the holotype of *Litoria subglandulosa* (SAMA R13504), a female, was collected along with 24 males of group 2, making it likely that the name *L. subglandulosa* is correctly applied to this group. For the purposes of describing the two groups, *a priori* unclassified females from locations where male(s) had been identified by either

allozymes or DFA were classified as the same group as those male(s). However, specimens from locations from which only *a priori* unclassified females were available were not included in the descriptions.

Systematics

The two groups represent distinct evolutionary lineages. Each is defined by apomorphic allozyme character states in at least one locus. Mitochondrial haplotypes from the two groups were reciprocally monophyletic with approximately 2.3% sequence divergence between lineages for the relatively conservative *16S rRNA* gene and 7.4% for the more rapidly evolving *ND4*. The mtDNA divergence together with the allozyme differentiation could indicate a substantial period of evolutionary divergence. Furthermore, each group is clearly distinct in shape as exemplified by the very high percentage correct classification in the DFA in spite of the overlap in adult male size. We regard these groups as separate evolutionary lineages, possibly of long-standing, and therefore distinct species under the evolutionary species concept (Simpson, 1951; Wiley, 1978; Frost & Hillis, 1990). The type locality of *Litoria subglandulosa* is within the geographic range of group 2, hence the name *L. subglandulosa* is applied to this taxon. As there are no other names available (Cogger *et al.*, 1983) we describe group 1 as a new species, *L. daviesae*.

Litoria daviesae n.sp.

Type data. HOLOTYPE, AMS R153052, an adult male from Cobcroft's Trail, Werrikimbe National Park, New South Wales, $31^{\circ}13'30"S$ $152^{\circ}10'12"E$ (Australia 1:25,000 series sheet 9335-IV-S, grid reference 420465444), collected by M. Mahony, R. Knowles and S. Donnellan on 13 November 1993.

Other material examined. See the Appendix for details of other specimens examined. These specimens are not paratypes.

Diagnosis. A member of the *Litoria citropa* species group characterized by the presence of submandibular gland, reddish-orange colouration of inguinal region and posterior surface of the lower limbs. Can be distinguished from all other members of the *L. citropa* species group except *L. citropa* and *L. subglandulosa* by the presence of the prominent supratympanic fold and submandibular gland. Can be distinguished from *L. citropa* by the absence of vocal sac (present in *L. citropa*), hidden tympanum (distinct in *L. citropa*), dorsum either with or without sparsely distributed, small, raised "warts" in *L. daviesae* versus frequent small, raised "warts" with black pigmentation to distal end in *L. citropa*. Can be distinguished from *L. subglandulosa* by a combination of lightly shagreened skin texture in a majority of *L. daviesae* versus smooth skin in *L. subglandulosa*. In life, the colour of *L. daviesae* "ranges from uniform golden brown with scattered darker mottling over the dorsum to specimens with some small areas of green",

Table 2. Variable sites among 11 aligned nucleotide sequences from *Litoria*. A, *16s rRNA* and B, *ND4*.

A—16S rRNA

[illegible]

B—ND4

[illegible]

whereas *L. subglandulosa* is “predominantly green” (“southern” versus “northern” localities respectively in Anstis & Littlejohn [1996]); and larger adult size: *L. daviesae* SV ♂♂ 38.7–53 mm, ♀♀ 59–63.4 mm versus

L. subglandulosa SV ♂♂ 34.5–40.3 mm, ♀♀ 45.8–50.4 mm. An unpaired Student's *t* test showed a highly significant difference between the means of the SV of ♂♂ ($t = 8.42$, $df = 52$, $P < 0.0001$).



Figure 3. An adult male (SAMA R51059) *L. daviesae* n.sp. from the Ellenborough River, New South Wales photographed in life.

Description of holotype. Head approximately as long as broad (HL/HW 1.04), and approximately one third snout to vent length (HL/SV 0.38). Snout prominent, blunt when viewed from above and in profile. Nostrils more lateral than superior, closer to snout than to eye. Distance between eye and naris equal to internarial span (EN/IN 1.08). Canthus rostralis well defined and straight. Eye relatively large, its diameter greater than eye to naris distance. Pupil horizontal when constricted. Tympanum small, indistinct, and oval with long axis tilted towards eye. Tympanum length approximately half eye diameter (T/E 0.45). Well-developed supratympanic fold, glandular in appearance, that partially obscures tympanic region. Vomerine teeth long curved plates directed posteriorly from the front margin of the choanae. Tongue approximately rectangular.

Fingers long, slender, unwebbed. Subarticular and palmar tubercles prominent. Terminal discs expanded, extending beyond lateral extremities of penultimate phalanx. Fingers in order of length $3 > 4 > 2 > 1$. Hindlimb length moderate (TL/SV 0.58). Toes in order of length $4 > 5 = 3 > 2 > 1$. Webbing reaches base of second most distal phalanx on toe 4 and penultimate phalanx on other toes. Subarticular tubercles prominent. Small oval inner metatarsal tubercle present.

Terminal toe discs slightly expanded, just extending beyond lateral extremities of penultimate phalanx.

Dorsum lightly shagreened. Abdomen, undersurface of thighs, submandibular area and lateral aspect of body mildly granular. There is a broad and prominent gland covered by smooth skin around the margin of the submandibular area. Pectoral fold and vocal sac are absent.

Dimensions of holotype (mm) SV 44.3, HL 15.4, HW 15.1, EN 3.7, IN 2.8, E 4.5, T 1.9.

Colour in preservative. Base colour of dorsum uniform dark grey, with some small black speckles from base of head to vent. Upper surfaces of limbs same base colour as dorsum and lightly speckled with black. Dark grey base colour of dorsum becomes patchy on lateral aspect of body as base colour is replaced by lighter grey tone, eventually being replaced by flesh colour on venter. Upper lip margin bordered by fine cream line extending from snout to end of jaw where it is expanded. Anterior surface of thigh flesh coloured, without patterning. Venter and undersurfaces of hands and feet cream, throat lightly suffused with light gray wash, edge of mandible dark gray.

Variation. SV of adult ♂♂ ($n = 22$) measure 38.7–53 mm and ♀♀ ($n = 2$) 59–63.4 mm. Head length equal to head breadth (HL/HW 1.06 ± 0.06 , range 0.94–1.18). Head length approximately $\frac{1}{3}$ snout to vent length (HL/SV 0.38 ± 0.02 , range 0.35–0.41). Hind limbs short (TL/SV 0.53 ± 0.03 , range 0.45–0.57). Eye to naris distance to internarial ratio highly variable (EN/IN 1.16 ± 0.11 , range 0.94–1.4). Dorsum lightly shagreened in a majority of specimens. The description of variation of colour in life is based on colour transparencies of three specimens—SAMA R51053, R51055, R51059 (Fig. 3). Dorsum base colour pale brown with dark brown to black speckling variably present. Upper surfaces of limbs have similar colour pattern to dorsum. Loreal region from snout to angle of jaw light green bordered above along canthus rostralis by a black band beginning at snout, passing through eye, across the top of tympanum, over forelimb and broken into black speckling by the intrusion of the dorsal and lateral colours posterior to forelimb. A prominent white stripe along upper lip, starting at snout and continuing for length of jaw, expanding slightly at posterior margin of jaw. Inguinal region, anterior and posterior surfaces of limbs yellow brown or orange. Iris golden.

Etymology. Named in honour of Margaret Davies, Zoology Department, University of Adelaide for her substantial contribution to the advancement of herpetology in Australia and the systematics of Australian anurans.

Distribution and habitat. Known from 14 locations in central-eastern to lower-northeastern New South Wales from north of the Hunter River to the catchment of the Hastings River—a distance of about 150 km (Fig. 1) (NSW NPWS, 1994; Anstis, 1997). All sites were streams above 400 m elevation. Adults are found adjacent to permanently flowing streams, which usually consist of sections of large pools with gentle flow interspersed with faster flowing shallow sections with cascades and waterfalls. On the tablelands the surrounding vegetation may be heath or dry open forest and along the streams the dominant vegetation is tea tree (*Leptospermum* species) with tussocks (*Lomandra* species) and various ferns. Streams on the edge of the escarpment and in deeper gullies are dominated by wet sclerophyll and rain forest vegetation, usually with a rainforest understorey.

Key to the larger members of the *Litoria citropa* species group

- 1 No supratympanic fold or submandibular gland *Litoria phyllochroa* complex
- Prominent supratympanic fold and submandibular gland present 2
- 2 Vocal sac present; adult ♂♂ SV 46.9–56.6 mm, adult ♀♀ SV 56.5–61.8 mm; tympanum obvious; frequent small, raised “warts” with black pigmentation to distal end *L. citropa*
- Vocal sac absent; hidden tympanum; adult ♂♂ SV 38.7–53 mm, ♀♀ SV 45.8–63.4 mm 3
- 3 Lightly shagreened skin texture in majority of specimens; colour in life ranges from uniform golden brown with scattered darker mottling over dorsum to specimens with some small areas of green; adult ♂♂ SV 38.7–53 mm, adult ♀♀ SV 59–63.4 mm *L. daviesae*
- Smooth skin; colour in life predominantly green; adult ♂♂ SV 34.5–40.3 mm, adult ♀♀ SV 45.8–50.4 mm *L. subglandulosa*

Discussion

Litoria daviesae and *L. subglandulosa* represent sibling species that are very similar in external morphology. The species have few mutually exclusive character states. However, the species are clearly genetically well differentiated as exemplified by the divergence at allozyme loci and among mitochondrial nucleotide sequences. The relatively frequent occurrence of similar “cryptic” species pairs or complexes in the eastern Australian anuran fauna (Martin *et al.*, 1979; Donnellan *et al.*, 1999) suggests the

need for a comprehensive screen of wet forest fauna with a combined molecular and morphological approach.

The habitats of *Litoria daviesae* and *L. subglandulosa* are very similar. These species have rarely been detected away from the riparian zone, and the implication is that they rely on habitats within this zone for breeding and foraging. Detailed studies of microhabitat use are necessary to determine the potential effects that changes to riparian habitats may have on the continued persistence of these frogs. Nothing is known about habitat use outside of the breeding season.

Breeding biology. Anstis & Littlejohn (1996) described various aspects of the male advertisement call and oviposition sites of *Litoria daviesae* (specimens from their locations 1–9). When calling, adult males can be found singly or in small numbers at suitable sites along streams. Anstis & Littlejohn (1996) could not distinguish the male advertisement calls of *L. daviesae* (their “southern *L. subglandulosa* localities”) and *L. subglandulosa* (their “northern localities”), but they were not explicit in describing how they compared the calls. Aside from small differences in body proportions, the larvae of the two species are apparently similar sharing a larval mouthpart morphology, originally described by Tyler & Anstis (1975), which is unique among Australo-Papuan hylids (Anstis & Littlejohn, 1996).

Assessment of historical and current distribution and conservation status of *Litoria daviesae* n.sp. and *L. subglandulosa*. *Litoria subglandulosa sensu lato* is reported to have declined from sections of its distribution and following assessment of its conservation status (Lunney *et al.*, 1996b), was listed as “vulnerable” under the NSW Threatened Species Conservation Act, 1995. In recognizing that this taxon comprises two species, it is desirable to readdress the conservation status of the constituent taxa.

Because most populations of *Litoria daviesae* have been detected only in the past five years (Anstis & Littlejohn, 1996) it is difficult to make a relative assessment of the past and present distribution and abundance of the species. The species is known from 18 different localities. The earliest collections are from near Elands on the Comboyne Plateau and the Williams River in Barrington Tops NP collected in 1972 and 1976 respectively. It is apparent that the species has a restricted distribution. If the species were formerly more widespread it would have been detected more widely as most of the locations from where it is known and areas adjacent to them have had access via forestry roads for many years. It is also apparent that the species is not abundant. Collections from individual locations are small and reports of the species usually refer to small populations (Tyler & Anstis, 1975; Anstis & Littlejohn, 1996). This may, however, be partially due to a restricted breeding period as at six sites in Barrington Tops and Werrikimbe National Park 14–55 frogs were observed in 1993–1996 (Anstis, 1997; present study). Lastly, it appears the species occurs only in a limited range of habitats; there are no records of the adults away from upland streamside habitats, and they do not occur below elevations of about 400 m.

To assess the conservation status of *L. daviesae* n.sp. we used the scoring system reported by Lunney *et al.*, (1996a) as follows. The species has a limited distribution. It occurs in a narrow band on the eastern edge of the tablelands and great escarpment of the Great Dividing Range, with a latitudinal range of about 150 km and a narrow east-west distribution. Because previous information on the distribution and abundance of this species is limited, it is difficult to assess whether the species is in decline. However, Anstis (1997) reported reduced population abundance in the region between the Hastings and Manning Rivers. Furthermore, clearing for agriculture has occurred over large

areas that were likely to formerly lie within the distribution of this species, particularly in the regions of the Comboyne Plateau and upper Manning River catchment. Forestry occurs at many of the sites where the species is currently known and the short and long-term impacts of various practices have not been assessed. In addition many of the streams within the species’ range have been stocked with exotic fish such as carp (*Cyprinus carpio*), trout (*Oncorhynchus* and *Salmo* species) and mosquito fish (*Gambusia holbrooki*), and while there have been no explicit studies of the impact of these fish on the frog there are several studies which indicate they may have a negative impact on eggs and larvae of stream frogs (Harris, 1995; Webb & Joss, 1997). Lastly, this species is a member of a species group that has experienced declines and disappearances from an as yet unidentified cause (Mahony, 1996). The small geographic range of the species, its dependence on unpolluted upland stream habitats (Anstis, 1997), the occurrence of considerable habitat loss and fragmentation within its range, and the apparent isolation of the known populations leads to it being categorized as “vulnerable”.

With the recognition of *Litoria daviesae* n.sp., the geographic range of *L. subglandulosa* is reduced. It is now known only from stream habitats on the eastern escarpment of the Great Dividing Range from the “The Flags” near Walcha in the south to Girraween National Park in the north, a distance of about 250 km. Within this range it appears to occur in disjunct populations, usually at high altitude. It is generally associated with well-vegetated, upland streams above 600 m elevation in a similar range of forest types to *L. daviesae* (NSW NPWS, 1994).

We used the scoring system reported by Lunney *et al.*, (1996a) in the following assessment of the conservation status of this species. *Litoria subglandulosa* has disappeared from several localities in the south of its range. Despite extensive searches no populations have been detected since 1978 in the New England National Park and surrounding areas (Anstis, 1997), or farther north in the headwaters of the Oban and Henry Rivers. The species was once common there as the species was recorded on numerous occasions in the early 1970s during a period of active field collection (Heatwole *et al.*, 1995; Australian Museum Register). Disappearance of frogs from these areas occurred sometime after the mid 1970s. During the past five years the only populations detected in this southern portion of the former distribution were in the eastern catchment of the Guy Fawkes River (present study), in the Warra State Forest east of Ben Lomond, and in the Styx River State Forest (NSW NPWS, 1994). The Northeast Forest Biodiversity Survey conducted by the NSW NPWS from September 1991 to May 1993, which included two spring-summer seasons when the animals are known to be active and breeding, surveyed 573 sites in northeast New South Wales using standardized methods (NSW NPWS, 1994). The region covered by this major survey encompassed the range of *L. subglandulosa sensu lato*, and the habitat of this species was systematically surveyed by nocturnal streamside searches, and included targeted survey methods such as male response to call broadcast. The species was detected on only

eight occasions. In the northern portion of the species range it has been observed in recent years in Gibraltar Range and Washpool National Parks and further north in the Forestlands and Spirabo State Forests and on the Timbarra Plateau (present study; Mahony, unpubl. data). The preferred habitat of the species is the streams that drain east of the Great Dividing Range, in the section of the streams where they begin to descend the great escarpment. The species does not appear to occur any longer in the upper reaches of many of these streams that originate on the tablelands. On the tablelands many streams are predominantly surrounded by cleared agricultural land, are polluted by agricultural and urban by-products, have altered flow regimes and contain introduced predatory fish. The precise impacts of these changes on the frogs and their larval stage are unknown. Combined with its small geographic range, the occurrence of habitat loss and fragmentation within its range, and the apparent isolation of the known populations, leads to *L. subglandulosa sensu lato* being categorized “vulnerable”.

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Appendix

Specimens examined. Unmarked specimens were examined for morphology only, specimens marked ^a were examined for morphology and allozyme electrophoresis, specimens marked * were examined for morphology and allozyme electrophoresis and mtDNA, specimens marked ^m were examined for mtDNA only. Abbreviations in bold refer to OTU codes mentioned in the text. Institutional abbreviations follow Leviton *et al.* (1985) except for ABTC—Australian Biological Tissue Collection, South Australian Museum, Adelaide. All locations are in New South Wales unless indicated otherwise.

Litoria citropa: Endrick R. SAMA R42608*, R42609*; Wombeyan R. ABTC 7146^m (no voucher).

Litoria pearsoniana-1: Emu Ck, Qld SAMA R33652^m.

Litoria pearsoniana-2: Doyles River SF ABTC 26055* (no voucher); Allyn R. ABTC 25688^m.

Litoria phyllochroa: Roseville ABTC 25677^m.

Litoria nudidigitus: Aberfeldy R., Vic. ABTC 60187^m.

Litoria subglandulosa: **Girr**: Girraween, Qld QM J31487–9, ABTC 68396^m, 68397^m, 68398^m (no vouchers); **Timb**: Timbarra Plateau SAMA R51051*; **Gibr**: Dandahra Creek, Gibraltar Range NP SAMA R39108*; Gibraltar Range NP QM J31490–2, J40012, J55262–3; **Dorr**: Wild Cattle Creek SAMA R51052*; Sandys Ck Dorriggo AMS R52391; Barwick Creek, near Ebor SAMA R13303, R13504–10, R13060, QM J17025, J27495; 11km S Ebor QM J18044; Styx River QM J26028; Little Styx River, near Point Lookout SAMA R13626–39, R13677–80; Point lookout AMS R17577, R42933, R51097, R51104, R51736–7, R51739–41, R52630; The Flags AMS R37017.

***Litoria daviesae* n.sp.**: **Werr**: Werrikimbe National Park SAMA R51053*, R51054*, AMS R153052*; Mt Boss SF AMS R108692; **Doyle**: Doyles River SAMA R51055, ABTC 26058*; **Royal**: Mount Royal SAMA R51056*, R51057*, R51058*; **Ellen**: Ellenborough River SAMA R51059*; Bulga SF AMS R104932; **Elands**: Elands ABTC 7088^a (no voucher); Sharpes Creek, Gloucester Tops SAMA R51060* (typed for diagnostic loci only); Barrington Tops SF AMS R76519–20; **Dilg**: Dilgry R. SAMA R51061*, R510612*, R510613*, AMS R148831; Upper Allyn River AMS R31683; Williams River, AMS R144861–2; Dingo Tops SF AMS R148855; Tuggalo SF AMS R150090. **Specimens not assigned**: New England NP AMS R35525, Oaky Ck AMS R36724, Gibraltar Range NP AMS R96910, Forbes R. AMS R103080.

Litoria spenceri: Big River, Vic. SAMA R47504*; White Creek, Vic. SAMA R45359*; Howqua River, Vic. SAMA R47485*; Bundarra R., Vic. SAMA R43767^m, Bogong Creek SAMA R47674*.

Litoria caerulea: SAMA R33448 Townsville, Qld.

Formation of Chrysocolla and Secondary Copper Phosphates in the Highly Weathered Supergene Zones of Some Australian Deposits

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ABSTRACT. Intense weathering of copper orebodies in New South Wales and Queensland, Australia has produced an unusual suite of secondary copper minerals comprising chrysocolla, azurite, malachite and the phosphates libethenite and pseudomalachite. The phosphates persist in outcrop and show a marked zoning with libethenite confined to near-surface areas. Abundant chrysocolla is also found in these environments, but never replaces the two secondary phosphates or azurite. This leads to unusual assemblages of secondary copper minerals, that can, however, be explained by equilibrium models. Data from the literature are used to develop a comprehensive geochemical model that describes for the first time the origin and geochemical setting of this style of economically important mineralization.

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Recent exploitation of oxide copper resources in Australia has enabled us to examine supergene mineral distributions in several orebodies that have been subjected to intense weathering. These include deposits at Girilambone (Gilligan & Byrnes, 1994) and Goonumbla or Northparkes in NSW (Heithersay *et al.*, 1990; Crane *et al.*, 1998) and several smaller deposits in the Mt. Isa Block in northwest Queensland (Ball, 1908; Day & Beyer, 1995; Carter *et al.*, 1961). Consequences of the intense weathering of these deposits include the mobilization of silica and subsequent formation of considerable quantities of chrysocolla and secondary silica in the oxidized zones. Furthermore, all of

these deposits are characterized by an abundance of the secondary copper phosphates libethenite and pseudomalachite associated with smaller amounts of cornetite and turquoise.

Although the secondary mineral distributions in these deposits vary, a number of recurring paragenetic relationships are evident. The copper carbonates malachite and azurite are seldom replaced by chrysocolla, nor are the secondary copper phosphates. Chrysocolla and/or secondary silica frequently envelop copper carbonates and phosphates, the more stable phases in such environments. Characteristic zoning of the phosphate minerals has also been noted, with

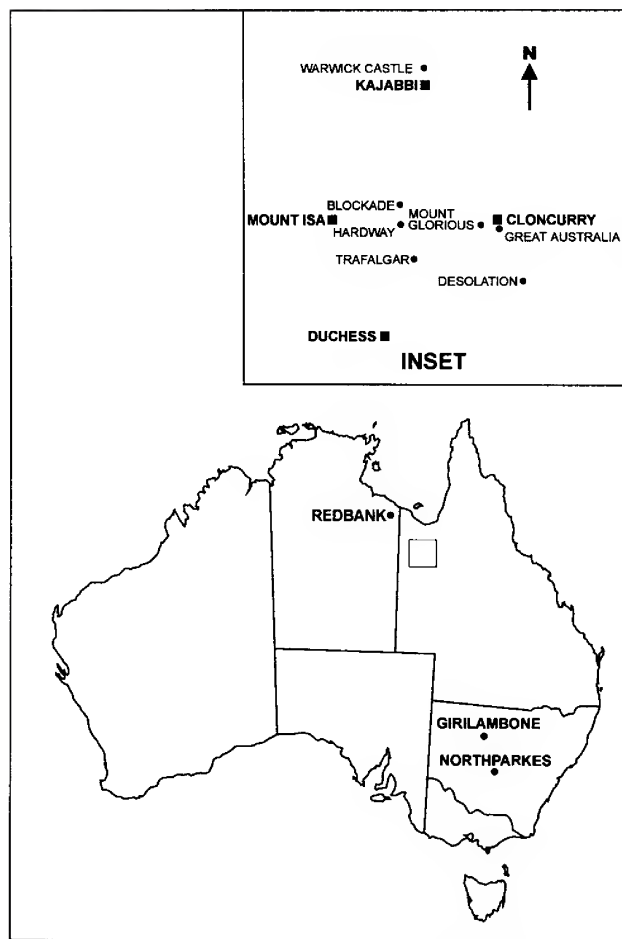


Figure 1. Locations of the deposits included in this study.

libethenite invariably being found nearer the surface. Repetition of these observations across a number of sites has prompted an investigation into the equilibrium chemistry of these minerals. An equilibrium approach was found to explain many of the parageneses noted, and the findings appear to be characteristic of the type of oxidized mineral zones involved. The locations of the deposits studied are shown in Figure 1.

Phosphate minerals

The distribution of secondary copper phosphates in the Northparkes orebodies has been described previously by Crane *et al.* (1998). Here libethenite $[\text{Cu}_2\text{PO}_4(\text{OH})]$ and pseudomalachite $[\text{Cu}_5(\text{PO}_4)_2(\text{OH})_4]$ are the dominant copper minerals at the base of extensively leached kaolinized zones and are associated with secondary silica, chrysocolla (*vide infra*) and malachite, $[\text{Cu}_2\text{CO}_3(\text{OH})_2]$. Particularly noteworthy are rhythmically banded, botryoidal malachite-pseudomalachite composites comprised of individual layers up to a few tenths of a millimetre thick. Similar material has been recovered from the upper sections of the Main Lode at the Great Australia mine, Cloncurry (Day & Beyer 1995) where, in the outcrop, the malachite had been leached

from the composites to leave shells of pseudomalachite (Fig. 2). Similar rhythmic banding involving the same minerals was noted in the upper sections of the oxidized zone of the Warwick Castle lode, north of Kajibbi.

With respect to replacement textures, pseudomorphs of pseudomalachite after azurite have been collected from the 10271 bench in the E27 deposit at Northparkes (Crane *et al.*, 1998). Other material shows pseudomalachite as a coating of crystal aggregates over azurite crystals and in some instances, the azurite has subsequently dissolved to yield pseudomalachite endomorphs.

A separate, but remarkable, observation in many of the deposits is the zoning of the secondary copper phosphates in the supergene profile. In particular, libethenite is always found near the top of the oxidized zone. At Northparkes, weathering of the host quartz monzonite porphyry has produced bleached, kaolinized zones from which all visible traces of copper mineralization have been removed (Crane *et al.*, 1998). Immediately beneath these zones, pseudomalachite and libethenite are associated with secondary manganese oxides. Libethenite is limited to the top contact of the oxidized zones with pseudomalachite persisting a few metres deeper and grading into more conventional malachite—azurite and then cuprite—native copper—chalcocite assemblages.

Kaolinization of host rocks at Girilambone and Great Australia, chlorite sericite schists and metadolerites, respectively, is of more limited extent than at Northparkes, and results from sulphuric acid generation as the result of the oxidation of pyrite. In both deposits, secondary copper phosphate mineralization was extensive.

Pseudomalachite and libethenite were present in the outcrop of the Great Australia Main Lode, with the former occurring abundantly as casts in friable goethite-hematite gossan. Libethenite was found near the surface, both in vughs in ferruginous quartz and also associated with pseudomalachite and cornetite, in vughs in altered tuffs. As mining of the oxide zone proceeded, abundant libethenite was found in and immediately beneath the silicified gossan of the Main Lode, particularly towards the northern end of the main open cut. Aggregates of acicular and etched crystals to 10 mm were scattered over joints and fractures and in vughs in ferruginous lode quartz and in silicified gossan, sometimes accompanied by turquoise. However, all traces of libethenite had vanished at a depth of about 15 m. Pseudomalachite, occurring as crystal aggregates or bunches coating vughs in friable gossan and as banded botryoidal material associated with malachite, persisted to the base of bench 11 (c. 35 m from surface) in the Main Lode. Little phosphate mineralization was noted in the intersecting B Tangye Lode.

At Girilambone, coarsely crystallized libethenite (as prisms to 2.5 cm) was confined to a zone extending from 10 to 18 m from the surface, particularly in friable quartzite gossan. Occasional spherules and coatings of turquoise were present in this material. In contrast, pseudomalachite was a comparatively common secondary phase in the main pit at Girilambone and extended through the libethenite zone to Bench 28, approximately 90 m from the surface. It principally occurred in or near the quartzite gossan as crystal



Figure 2. Pseudomalachite casts; Main Lode outcrop, Great Australia mine, Cloncurry, Queensland. The field of view is c. 8 cm across.

aggregates and bunches and as occasional stalactites mixed with malachite. Often, single crystals of azurite were embedded in the pseudomalachite; azurite was always a frequent associate.

In other copper deposits in the Mt. Isa Block, the same zoning is evident. At Warwick Castle, libethenite as acicular and platy crystals to 8 mm liberally coated shattered lode quartz and joints in altered metabasalts in the lode outcrop, associated with minor pseudomalachite and chrysocolla. Libethenite was confined to a near surface (<10 m) zone, with pseudomalachite, occurring as crystal clots and rhythmically banded aggregates with malachite, persisting deeper than 30 m (190 RL bench). Here it was also present as coatings of crystal aggregates on quartz-rich gossan associated with chrysocolla and azurite. Similarly, multiple generations of libethenite and pseudomalachite were confined to the top-most sections of the Sandy Flat pipe at Redbank, Northern Territory, at the northwest extremity of the Mt. Isa Block (McLaughlin *et al.*, 2000). At the Hardway mine, near Mt. Isa, libethenite associated with pseudomalachite occurs in a kaolinized quartz-rich gossan at the surface and persisting to a depth of a few metres in a small open cut. At the Desolation prospect, south of Cloncurry, libethenite and pseudomalachite occur in small pits within a metre of the surface, associated with malachite, chrysocolla and the secondary arsenates olivenite $[\text{Cu}_2\text{AsO}_4(\text{OH})]$, conichalcite $[\text{CaCuAsO}_4(\text{OH})]$, and clinoclase $[\text{Cu}_3\text{AsO}_4(\text{OH})_3]$, these arsenates being the result of oxidation of arsenopyrite, cobaltite and chalcopyrite.

Chemical relationships of the phosphate minerals

Thermodynamic data for libethenite, pseudomalachite and cornetite $[\text{Cu}_3\text{PO}_4(\text{OH})_3]$ and the equilibrium relationships of these minerals with malachite and azurite $[\text{Cu}_3(\text{CO}_3)_2(\text{OH})_2]$ (Magalhães *et al.*, 1986, 1988), show that, in general, equilibrium paths between the copper phosphates and the carbonates are restricted. Thus, whilst routes are available for pseudomalachite and cornetite to azurite transformations, and for cornetite to malachite transformations, malachite and pseudomalachite cannot directly replace each other, because of thermodynamic constraints, under normal supergene conditions. Intermediate steps involving azurite or cornetite are necessary, thus making malachite-pseudomalachite assemblages quite stable under conditions in which appropriate kinetic factors operate.

This appears to be the case with the deposits mentioned above in that the rhythmically banded malachite—pseudomalachite simply reflects the fluctuating availability of $\text{H}_2\text{PO}_4^{2-}(\text{aq})$ or $\text{HPO}_4^{2-}(\text{aq})$ versus $\text{HCO}_3^{-}(\text{aq})$ or $\text{CO}_3^{2-}(\text{aq})$ in mineralizing solutions. When more phosphate was present, pseudomalachite would form because of its lower solubility (although perhaps *via* a thin and subsequently pseudomorphed layer of cornetite). Weathering of malachite-pseudomalachite aggregates to leave pseudomalachite as thin casts probably represents the result of similar solubility differences to those mentioned above, as well as to the fact that pseudomalachite dissolves reversibly

in weakly acid solutions much more slowly than does malachite, the latter involving loss of $\text{CO}_2(\text{g})$.

The rare occurrence of cornetite, confined to the Great Australian Main Lode outcrop (Day & Beyer 1995) in the deposits examined, is due to its formation under somewhat more unusual chemical conditions (relatively higher pH, higher copper and lower phosphate ion activities) compared to those responsible for the crystallization of pseudomalachite and libethenite (Magalhães *et al.*, 1986, 1988). Considerable variation in these parameters at the Great Australia deposit is evidenced by the presence of all possible parageneses of these minerals in the outcrop of the Main Lode. Reference to the equilibrium pH-activity diagram in Figure 3 (Magalhães *et al.*, 1986, 1988) suggests that the occurrence of cornetite at this locality may be related to higher pH regimes, since the outcrop occurs in the vicinity of carbonate rocks of the Corella Formation.

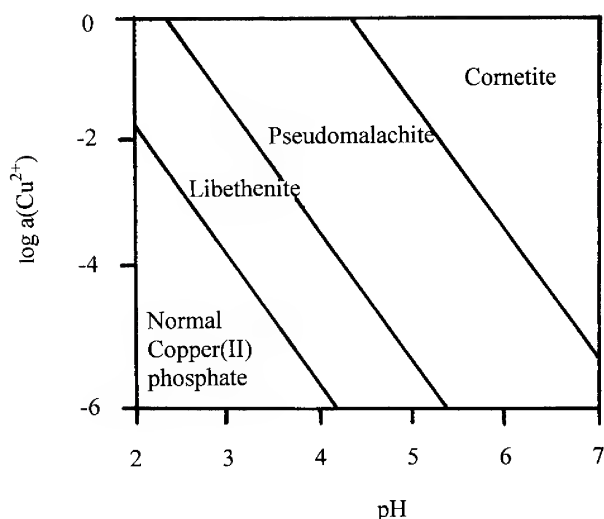


Figure 3. Equilibrium pH- Cu^{2+} activity diagram showing stability fields of the secondary copper phosphates at 25°C. Boundary conditions refer to equations written so that dihydrogen phosphate ion activity is not a variable.

Field observations above support the conclusion that libethenite typically occurs in the upper part of the oxidized zone, with pseudomalachite forming further down. The reason for this is not readily apparent from an inspection of equilibrium relations (Fig. 3), although it does explain the rarity of cornetite by fact that it can only form under comparatively basic conditions. However, the equilibrium relations can be recast in such a way that the observed zoning is easily understood, as shown in Figure 4. Here the constraints of pH are such that $\text{H}_2\text{PO}_4^-(\text{aq})$ is the predominant phosphate species in solution. These relations now indicate that libethenite forms at the most concentrated phosphate activities, while pseudomalachite forms from solutions with lower amounts of dissolved phosphate. It is thus appropriate that the phosphate source be considered.

In a classical study of the weathering of a gneiss, Goldich (1938) found that apatite, the most probable source of phosphate for all the above species, was among the least

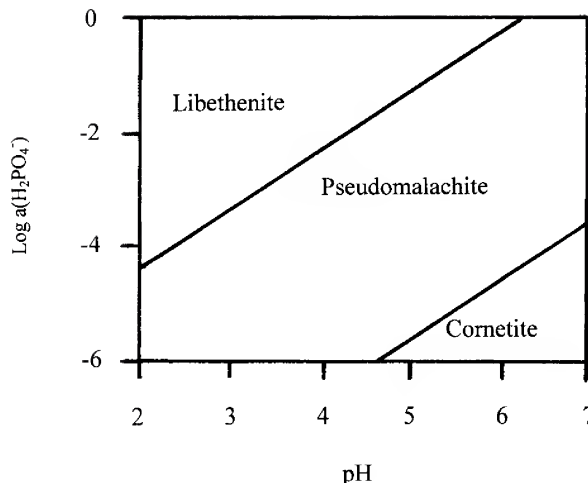
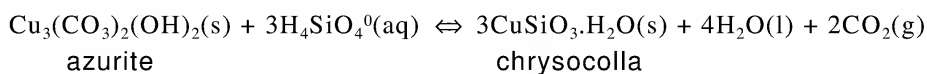


Figure 4. Equilibrium pH- $\text{H}_2\text{PO}_4^{2-}$ diagram for the secondary copper phosphate minerals at 25°C. Boundary conditions refer to equations written so that copper ion activity is not a variable.

stable minerals. Ollier (1984) noted that, of the apatite group, hydroxylapatite was most easily weathered and chloroapatite less so, while fluorapatite is somewhat more resistant to weathering. Thus the observed zoning of the copper phosphate minerals may simply be accounted for by the local phosphate distribution, related to variations in the intensity of weathering of the host rocks. The most intense weathering is usually at the surface and will lead to higher phosphate concentrations in downward-percolating groundwater, thus making the formation of libethenite more likely near the surface. As weathering intensity diminishes with depth, less phosphate will be available and pseudomalachite will dominate the secondary copper phosphates. This model, together with appropriate pH control, serves to unify all of the occurrences of the secondary copper phosphates in the deposits we have examined. Finally in this regard, Stumm & Morgan (1981) suggest that the formation of hydroxylapatite controls phosphate concentrations in groundwaters. At Northparkes, secondary hydroxylapatite is one of the last minerals to form in the oxidized zone and is commonly found as hexagonal plates to 1 mm on pseudomalachite and chrysocolla endomorphs after libethenite. No copper minerals were observed to form after hydroxylapatite (Crane *et al.*, 1998), suggesting depletion of copper with extended leaching.

Chrysocolla

Chrysocolla is a secondary copper silicate, which occurs abundantly in oxidized copper orebodies worldwide (Roberts *et al.*, 1990). However, its structure is poorly characterized as a result of its invariably quasi-amorphous nature. Van Oosterwyck-Gastuche & Grégoire (1971) proposed a chain structure for fibrous microcrystals from 0.5 to 3 microns long and 60–70 nm across, which corresponds with an idealized formula of $\text{Cu}_2\text{H}_2(\text{Si}_2\text{O}_5)(\text{OH})_4 \cdot n\text{H}_2\text{O}$. This formulation is supported by the work of Chukrov *et al.* (1968) and a number of analyses of chrysocolla containing



small amounts of other metals such as Al^{3+} substituting for Cu^{2+} , with charge compensation for Al^{3+} being maintained by variation of the number of protons present (Van Oosterwyck-Gastuche, 1970; Kiseleva *et al.*, 1991).

Chrysocolla specimens examined from the deposits discussed here and elsewhere give more or less broad reflections in X-ray powder diffraction (XRD) patterns, indicating variable degrees of order; all are cryptocrystalline and grade into copper-stained amorphous silica and quartz from sample to sample. At Great Australia, chrysocolla in the upper levels of the B Tangye Lode is more crystalline than chrysocolla encountered elsewhere, except for the Trafalgar deposit, south of Cloncurry (Fig. 1), and is comparatively ordered, as judged from the XRD pattern.

The end-member formula above is based on structural information but may be reduced to $\text{CuH}_2\text{SiO}_4 \cdot n\text{H}_2\text{O}$ or $\text{CuSiO}_3 \cdot n\text{H}_2\text{O}$, as has been written in the older literature. Newberg (1967) defined a partially dehydrated chrysocolla and gave its formula as $\text{CuSiO}_3 \cdot \text{H}_2\text{O}$. This formulation was used in his experiments to determine the thermodynamic properties of chrysocolla from solubility measurements. A value of the standard Gibbs free energy of formation, $\Delta_f G^\circ$, for amorphous chrysocolla was calculated as $-1206.7 \text{ kJ mol}^{-1}$ and $-1218.4 \text{ kJ mol}^{-1}$ for diopside as an "aged" chrysocolla precipitate, at 298.2K. Diopside, while it can be assigned a reduced stoichiometry of $\text{CuSiO}_3 \cdot \text{H}_2\text{O}$ as well, is however a crystalline monocyclosilicate of ring periodicity six. Its structure is well established by single-crystal X-ray studies (Ribbe *et al.*, 1977; Belov *et al.*, 1978). More recently, an accurate value for $\Delta_f G^\circ$ (diopside, s, 298.2K) has been reported (Kiseleva *et al.*, 1993) and a value of $-1220.8 \pm 4.6 \text{ kJ mol}^{-1}$ was derived *via* calorimetric measurements for the formula $\text{CuSiO}_3 \cdot \text{H}_2\text{O}$. The comparative rarity of diopside versus chrysocolla, must then be based on kinetic factors related to the ease and frequency of formation of appreciable amounts of the cyclic $\text{H}_{12}\text{Si}_6\text{O}_{18}$ polymer or its conjugate anions in solutions of silicic acid at low temperatures. Thus it is reasonable to take the more negative value of Newberg (1967) given above to represent cryptocrystalline chrysocolla. We have used this value in our calculations, which have proved to provide an explanation for many observations involving chrysocolla's paragenetic relationships.

The limits of concentration of dissolved silica in aqueous solutions at 25°C have been reviewed by many workers (Iler 1979; Stumm & Morgan 1981; Dove 1995) and continue to attract attention as new silica polymorphs are identified (Gisslason *et al.*, 1997). At 298.2K and 10^5 Pa , amorphous silica reaches an equilibrium concentration in water of $10^{-2.71} \text{ mol dm}^{-3}$ at neutral values of pH (solubility increases in basic solution as the contributions of conjugate anions of silicic acid become more important). For our considerations below, we have chosen this value to represent the maximum activity of silicic acid in water under these conditions; in thermodynamic terms, this is acceptable for calculations even though it is known that dimers are present as well (Dove 1995; Applin 1987).

Known relationships between the secondary copper carbonates and chrysocolla are comparatively simple, and have widespread application to observations of natural assemblages. First, at CO_2 pressures sufficiently high to make azurite stable with respect to malachite (c. $10^{-1.35}$; Williams, 1990), chrysocolla cannot replace azurite. Hence, for the equation shown above, at or above the given pressure, there is no achievable activity of $\text{H}_4\text{SiO}_4^0(\text{aq})$ such that azurite becomes unstable with respect to chrysocolla. Thus the remarkable examples of chrysocolla coating azurite at Northparkes (Crane *et al.*, 1998) appear to have formed simply by the later crystallization of chrysocolla on pre-existing azurite. Similar assemblages are found in the Queensland deposits mentioned previously, where azurite occurs near the surface.

However, mention should be made of reports of chrysocolla pseudomorphs after azurite and malachite (see, for example, Thompson 1980; Bywater 1984). Such observations are readily explained by reference to Figure 5 which shows that while azurite cannot be directly transformed to chrysocolla, malachite can be, and other conditions exist such that chrysocolla can only form coatings on pre-existing malachite. Thus, reported chrysocolla pseudomorphs after malachite are seen as arising simply from the existence of the appropriate chemical conditions, whereas reported chrysocolla pseudomorphs after azurite are in fact chrysocolla *after malachite* after azurite. Many specimens showing the formation of secondary silica and chrysocolla (especially in the upper sections of oxidized zones in the Mt. Isa Block) are known, the intense silicification of these bodies being directly related to the high degree of weathering of the enclosing rocks.

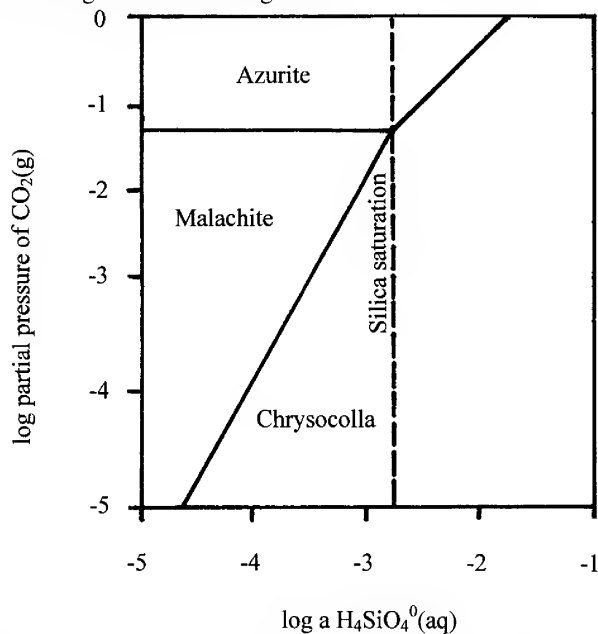


Figure 5. Stability fields for chrysocolla *versus* malachite and azurite at 25°C. The dashed line represents the limit of silicic acid activity in equilibrium with amorphous silica.

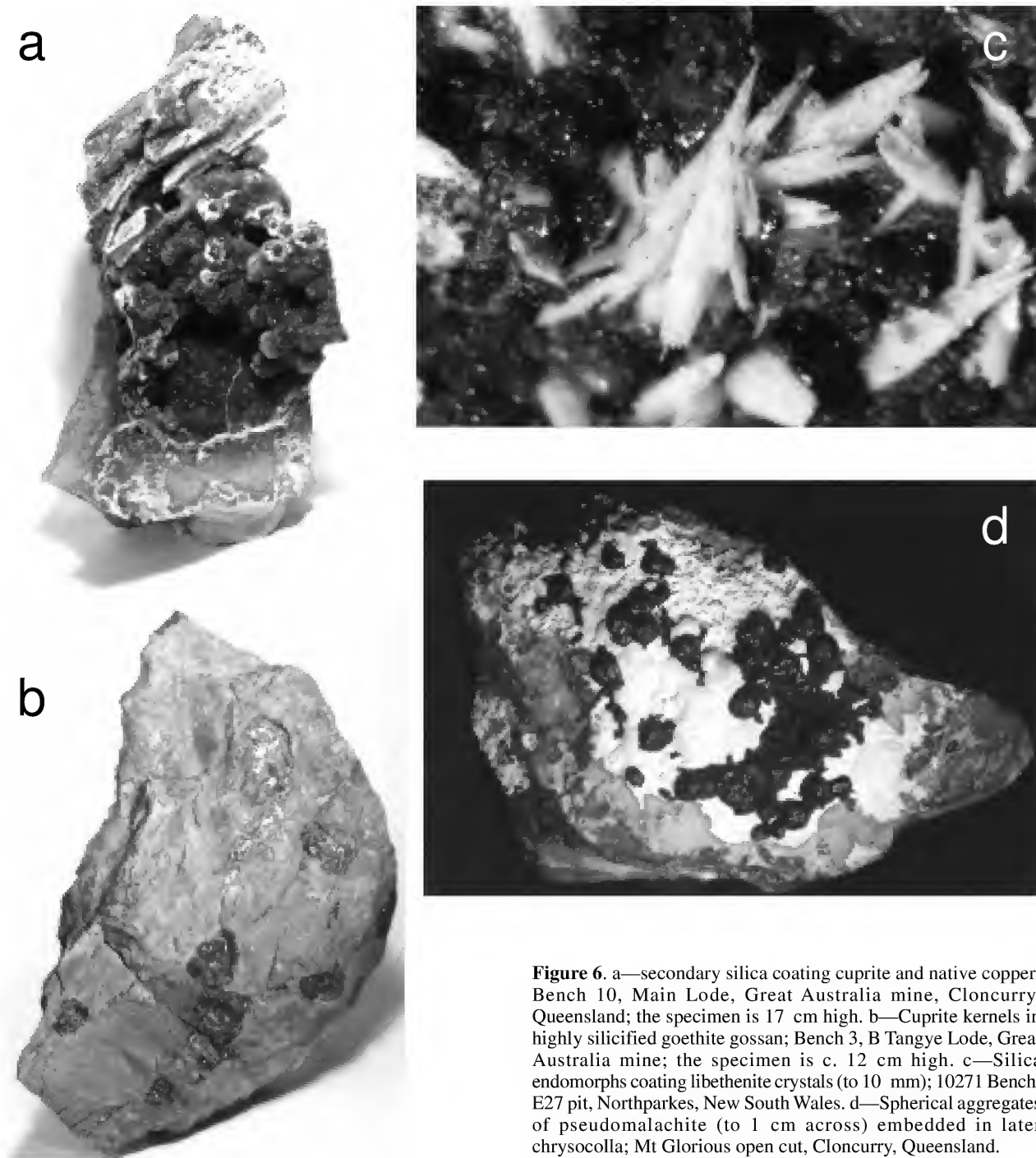


Figure 6. a—secondary silica coating cuprite and native copper; Bench 10, Main Lode, Great Australia mine, Cloncurry, Queensland; the specimen is 17 cm high. b—Cuprite kernels in highly silicified goethite gossan; Bench 3, B Tangye Lode, Great Australia mine; the specimen is c. 12 cm high. c—Silica endomorphs coating libethenite crystals (to 10 mm); 10271 Bench, E27 pit, Northparkes, New South Wales. d—Spherical aggregates of pseudomalachite (to 1 cm across) embedded in later chrysocolla; Mt Glorious open cut, Cloncurry, Queensland.

At the Great Australia mine, abundant secondary quartz, chalcedony and chrysocolla occur throughout the oxidized zone of the Main and B Tangye Lodes. In the former, secondary quartz completely enclosing otherwise unaltered malachite, cuprite and native copper crystals was common at depths below 20 m (Fig. 6a) and a completely silicified goethitic gossan was a feature of upper levels of the B Tangye Lode (Fig. 6b). Secondary silica infiltration of this section of the deposit gave a characteristic brown, cherty material studded with

kernels of native copper and cuprite, and occasional chalcocite and digenite, which had been rendered impervious to subsequent attack by aqueous solutions and persisted to within 10 m of the surface

Chrysocolla-coated malachite has been recovered from the Trafalgar, Warwick Castle, Desolation and Mt. Glorious deposits, and mines grouped around the Blockade mine, near Mt. Isa. Chrysocolla pseudomorphs after malachite are present in these deposits as well, especially at the Trafalgar mine.

Relationships between the secondary copper phosphates and chrysocolla are similar to the above in some respects, but more complex. Figure 7 shows equilibrium conditions calculated by the authors for these species, for pH values between 3 and 7, where $\text{H}_4\text{SiO}_4^0(\text{aq})$ and $\text{H}_2\text{PO}_4^-(\text{aq})$ are the dominant dissolved silica and phosphate species, respectively. Reference to this figure leads to a remarkable conclusion. There is no achievable $\text{H}_4\text{SiO}_4^0(\text{aq})$ activity when libethenite is the thermodynamically stable secondary copper phosphate, such that chrysocolla can replace libethenite. It must form together with it, when silica concentrations exceed saturation. Thus the phosphate-silicate assemblages from the upper levels of the Northparkes oxidized zones are explained. Silica and chrysocolla coat, but do not replace, libethenite (Fig. 6c). Subsequent dissolution of libethenite with changing solution chemistry has led to the preservation of chrysocolla and secondary silica endomorphs, as also seen in Figure 6. Again using Figure 7, the same explanation can be applied to the occurrence of chrysocolla and secondary silica on pseudomalachite, although saturated solutions of silicic acid do approach values which would lead to chemical attack. Phosphate values must fall to levels consistent with the stability of cornetite for chrysocolla to directly replace the copper phosphates. Abundant crystalline libethenite in the outcrop at the Hardway and Warwick Castle deposits further attest to the stability of libethenite over chrysocolla under all naturally achievable chemical conditions.

Many examples of the preservation of pseudomalachite in highly silicified secondary copper ores have been encountered. For example, it forms radiating crystal aggregates to 1 cm embedded in chrysocolla at Mt. Glorious (Fig. 6d). Chrysocolla and chalcedony coat and embed both pseudomalachite and libethenite in the Main Lode at the Great Australia Mine, and commonly in the Redbank and Trafalgar deposits.

Other relationships observed in the field can be attributed to kinetic factors. Rhythmically banded pseudomalachite–chrysocolla crusts from Northparkes are seen as arising from silica interaction with previously mentioned pseudomalachite–malachite assemblages (i.e., replacement of malachite by chrysocolla). The failure to observe pseudomalachite–cornetite transitions can be attributed to the preservation of chemical conditions such that pseudomalachite remains stable, coupled with the fact that compact crusts of pseudomalachite are rather slow to dissolve in aqueous solutions at room temperature (M.J. Crane and P.A. Williams, unpublished results). The preservation of pseudomalachite in the upper sections of oxidized ores of the Mt. Isa Block, particularly at Mt. Glorious and Great Australia is also due to this kinetic influence.

Conclusions

Sometimes unexpected assemblages of secondary copper phosphates with malachite, azurite and chrysocolla in highly weathered terrains can be explained using simple equilibrium models for mineral formation. Such models have been successfully applied to deposits at Girilambone

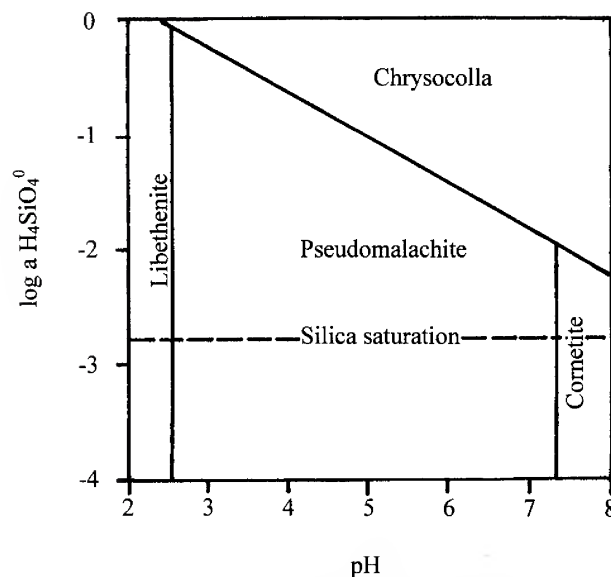


Figure 7. Stability field diagram for the secondary copper phosphates *versus* chrysocolla at 25°C. The dashed line represents the limit of silicic acid activity in equilibrium with amorphous silica.

and Northparkes, NSW, and to numerous oxidized copper lodes in the Mt. Isa Block, Queensland. The persistence of libethenite and pseudomalachite in these deposits is due to their particular chemical stabilities, which can be used to explain the development of pseudomorphous replacements of various kinds, especially those involving chrysocolla. For the first time, a comprehensive explanation of the chemical conditions responsible for the formation of this style of economically important mineralization has been provided.

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**Larvae of *Enchelyurus ater* (Günther, 1877)
and *E. kraussi* (Klunzinger, 1871)
(Pisces: Blenniidae: Omobranchini)**

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ABSTRACT The omobranchinid blennioid, *Enchelyurus ater*, ranges across the islands of the south Pacific Ocean, and *E. kraussi* ranges from the Red Sea to the Mariana Islands and eastern Australia. The planktonic larvae of these blennies were identified by establishing developmental series up to large larvae identifiable to species using morphological and meristic characters and geographic location. Larvae of both species are similar in appearance, hatch at about 1.5–2.5 mm length, and undergo notochord flexion at about 4.5–5.5 mm. *Enchelyurus ater* probably is near 12 mm, and *E. kraussi* probably nearer 15 mm, at settlement from the plankton. Larvae of both species have a rounded head, a short, coiled gut, an elongate, compressed tail, and about 34 myomeres. Small spines are present on the posterior preopercular margin at, or soon after, hatching. The spine at the preopercular angle becomes largest, reaching about 25% of head length in the postflexion stage. First the pectoral-fin rays, then principal caudal-fin rays, dorsal- and anal-fin anlagen, and pelvic-fin buds begin to form during the preflexion stage. All principal caudal rays are present by the end of the flexion stage. Pelvic-fin rays and all segmented dorsal- and anal-fin rays are present by mid-postflexion stage. Dorsal-fin spines and procurent caudal-fin rays form during the postflexion stage. Larvae of both species initially are pigmented dorsally on the head and gut, posteriorly on the ventral margin of the tail, and on the mesial surface of the pectoral-fin base. Pigmentation gradually increases on the head and gut in both and on the pectoral fin in *E. kraussi*, and decreases on the ventral margin of the tail in both.

Enchelyurus ater, *E. kraussi*, and the Hawaiian endemic, *E. brunneolus*, are a monophyletic group with unknown sister-species relationships. Larval characters suggest the hypothesis that *E. ater* is the sister species to *E. brunneolus*, and *E. kraussi* is the sister species to the other two.

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The blennioid genus *Enchelyurus* (tribe Omobranchini) comprises five species of small, demersal, Indo-Pacific nearshore reef fishes. Based primarily on similarities in dentition and colour pattern, Springer (1972) considered

three of these, *Enchelyurus ater* (Günther, 1877), *E. brunneolus* (Jenkins, 1903), and *E. kraussi* (Klunzinger, 1871), to be a monophyletic group, but he was unable to determine sister-species relationships among them

(Springer, 1982). *Enchelyurus kraussi*, apparently a species complex (V.G. Springer, pers. comm., August 1999), occurs in the Red Sea, the Gulf of Aqaba, the Indian Ocean, and the western Pacific Ocean as far north as Okinawa and east to the Mariana Islands, New Guinea, and Australia (Springer, 1982). *Enchelyurus ater* ranges throughout the oceanic islands south of the equator from Lord Howe Island and New Caledonia to the Tuamotu Archipelago (Springer, 1982). *Enchelyurus brunneolus* is endemic to the Hawaiian Islands (Springer, 1982), and thus is geographically remote from its nearest relatives.

Larval development of *E. brunneolus* was described by Watson (1987) and a transforming larva of *E. kraussi* was described by Kubo & Sasaki (2000). Nearly complete developmental series have been assembled for *E. ater* from the Tuamotu Archipelago, and for *E. kraussi* from eastern Australia, affording an opportunity to provide descriptions of the larval development of these species. In addition to the descriptions of larval development of *E. ater* and *E. kraussi*, the contribution of larval development to the interpretation of sister-species relationships in the *E. ater-brunneolus-kraussi* group is briefly considered.

Materials and methods

All specimens of *E. ater* were collected in February 1989 with an 83.5 cm mouth diameter, 0.5 mm mesh ring net towed in the upper 10 m of the water column (e.g., Leis *et al.*, 1991) of Rangiroa (c. 15°02'S 147°45'W), Takapoto (c. 14°36'S 145°12'W) and Takaroa (c. 14°20'S 145°W) lagoons, in the Tuamotu Archipelago, French Polynesia. Specimens of *E. kraussi* were collected with a variety of plankton samplers at various times in the 1980s at various eastern Australian locations, primarily from the vicinities of Lizard Island (14°41'S 145°27'E) and One Tree Reef (c. 28°30'S 152°05'E) on the Great Barrier Reef (Leis & Goldman, 1983; Schmitt, 1984), and from Lake Macquarie (c. 33°S 151°30'E) (Miskiewicz, 1987) and the northern coast of New South Wales (c. 29°S 154°E). Larvae generally were fixed in the field in 5–10% seawater formalin and stored in 2.5–5% formalin or 70% ethanol.

Descriptions are based on 101 *E. ater* (2.3–11.4 mm; recently hatched preflexion through late postflexion stages) and 25 *E. kraussi* (1.6–14.5 mm; recently hatched preflexion through late postflexion stages). All specimens were measured to the nearest 0.04 or 0.08 mm at 25× or 12×, respectively, depending on specimen size, using a Wild M-5 binocular microscope with an ocular micrometer. Dimensions measured included body length (BL), preanal length (PAL), body depth (BD), head length (HL), head width (HW), snout length (SnL), eye diameter (ED), length of spine at angle of posterior preopercular margin (PrSL), and lengths of pectoral (PIL) and pelvic (P2L) fins. These dimensions, as well as developmental states and body parts referred to in the descriptions, are defined by Moser (1996) and Leis & Carson-Ewart (2000). In the following descriptions references to larval length always refer to BL of preserved larvae, and descriptions of pigmentation refer solely to melanistic pigment. Size series of 17 *E. ater* and 15 *E. kraussi* were lightly stained with alizarin

red-S to aid in determining the sequence of fin development. Illustrations were made with the Wild M-5 microscope equipped with a camera lucida.

Identification. Larvae were identified by the series method. Late preflexion through late postflexion stage larvae were readily recognizable as belonging to the blennioid tribe Omobranchini on the basis of several meristic and morphological characters, especially head spination (e.g., Watson, 1983), and as *Enchelyurus* by their close resemblance to *E. brunneolus* (Watson, 1987). Briefly, larval *Enchelyurus* may be recognized by having a moderately broad head with short, rounded snout; a short, moderately broad gut (PAL usually c. 35–40% BL); a compressed tail; 33–36 myomeres; 13–16 (usually 14–15) pectoral-fin rays and VI–X (usually VII–IX) dorsal-fin spines; up to 6–7 preopercular spines, with the spine at the angle becoming longest by late preflexion stage (maximum length c. 25% HL, attained early in the postflexion stage); ornamentation (small prickles diminishing to low ripples and bumps) on the frontal, parietal, preopercular, articular and dentary bones; dorsal- and anal-fin pterygiophores lacking distal blades; and pigmentation primarily dorsally on the head and gut and on the ventral margin of the posterior half of the tail, with little or no pigment on the pectoral fins except commonly some on the pectoral-fin bases. *Enchelyurus ater* is the only *Enchelyurus* species (and the only representative of Omobranchini) known from the Tuamotu Archipelago, and myomere and fin-ray counts from the larger larvae from that location matched the vertebral and fin-ray counts of *E. ater* (e.g., Springer, 1972). Likewise, *E. kraussi* is the only *Enchelyurus* species reported from eastern Australia. At least seven other species of Omobranchini occur there as well, but all can be distinguished from *Enchelyurus* by meristic characters, for example by having more dorsal-fin spines and fewer pectoral-fin rays than *Enchelyurus* (e.g., Springer, 1972; Springer & Gomon, 1975). In addition, larval *Omobranchus* typically have a larger spine at the preopercular angle and more pigment on the pectoral fins and ventral margin of the tail, compared with *Enchelyurus*. Several *Omobranchus* species have prominent distal blades on the dorsal- and anal-fin pterygiophores (e.g., Watson & Miskiewicz, 1998; Kawaguchi *et al.*, 1999), lacking in *Enchelyurus*. Fin-ray and myomere counts from the larger eastern Australian *Enchelyurus* larvae matched the fin-ray and vertebral counts of eastern Australian *E. kraussi* (e.g., Springer, 1972).

Material examined. All specimens of *E. ater* and *E. kraussi* are deposited in the Ichthyology Collection, Australian Museum, Sydney (AMS I). In the following list, the registration number is given first (first five digits—station number, last three digits—lot number), followed in parentheses by the number and size range of specimens.

Enchelyurus ater (Günther, 1877). AMS I.29054-001 (3: 3.2–3.4 mm); I.29055-001 (5: 2.6–2.9 mm); I.29056-002 (3: 2.8–3.6 mm); I.29074-001 (5: 2.9–8.3 mm); I.29084-001 (2: 2.3–2.4 mm); I.29085-001 (4: 2.9–3.1 mm); I.29096-001 (14: 3.3–8.1 mm); I.29097-001 (16: 3.1–8.6 mm); I.29098-001 (16: 2.8–8.6 mm); I.29099-001 (10: 3.0–

5.4 mm); I.29100-001 (16: 2.8–5.6 mm); I.29101-001 (3: 4.1–5.0 mm); I.29103-001 (2: 3.3–3.7 mm); I.29104-001 (1: 4.4 mm); I.29123-002 (1: 11.4 mm).

Enchelyurus kraussi (Klunzinger, 1871). AMS I.21754-009 (1: 11.5 mm); I.21758-003 (3: 8.6–11.2 mm); I.23050-023 (1: 3.2 mm); I.23053-084 (1: 3.2 mm); I.23077-009 (2: 3.1–4.3 mm); I.23135-021 (1: 12.0 mm); I.23151-005 (1: 3.6 mm); I.25131-001 (1: 5.5 mm); I.28394-005 (1: 14.5 mm); I.30852-006 (2: 1.6–2.0 mm); I.33797-001 (2: 12.1–12.3 mm); I.33798-001 (1: 12.1 mm); I.39117-001 (1: 11.5 mm); I.39210-001 (1: 4.8 mm); I.39210-002 (4: 3.3–4.2 mm); I.39541-001 (2: 3.2–3.7 mm).

Larval descriptions

Enchelyurus ater (Günther, 1877)

Figs. 1, 2

Morphology. Least developed specimens (2.3–2.4 mm) had recently hatched, as evident in presence of small yolk sac containing remnants of oil globule and possibly yolk. These small larvae are well developed with open mouth, pigmented eyes, and first 2 preopercular spines forming. Notochord flexion begins at 4.9–5.0 mm, is completed between 5.2–5.6 mm. Largest specimen, 11.4 mm, nearing settlement stage as evident in resorption of preopercular spines (process underway but incomplete), presence of adult-type teeth, and development of cephalic sensory pore system. Springer (1972) listed juvenile (presumably settled) *E. ater* as small as 11–12 mm.

Initially, head broad and rounded, snout short and blunt, eyes oval to somewhat rectangular (elongate horizontally), coiled gut short, tail elongate and compressed. Changes in

most body proportions small during larval growth. Relative preanal length, head length, and snout length increase through early postflexion stage, then stabilize or decrease slightly. Relative body depth may increase slightly in postflexion stage (Table 1). Larvae become more compressed early in preflexion stage; relative head width stabilizes at about 70–80% HL by about 3 mm. Eyes become relatively smaller early in preflexion stage (Table 1), usually become round by beginning of notochord flexion. There are 34–36 myomeres (usually 34–35): commonly 6–7 preanal plus 27–28 postanal in preflexion stage larvae <4 mm, shifting to 9–10 preanal plus 24–26 postanal in flexion and postflexion stages (>5 mm).

First 2 preopercular spines located on anterior margin of lower limb and at angle of preopercle. A third spine added near upper end of upper limb before 3 mm. Maximum of 6–7 spines attained by about 4 mm. These persist through about 5.5 mm, then gradually decrease to 2–3 spines by late postflexion stage as smaller spines are resorbed or overgrown. Nearly 40% of larvae had more preopercular spines (usually 1) on one side (60% of these had more spines on right side). Early in preflexion stage spines are small and more or less evenly arrayed in single row along posterior preopercular margin. After 3 mm lowermost (= anteriormost) 1 or 2 spines, then spine at angle become longer than others. After 4 mm, spine at preopercular angle always longest, reaching maximum of about one-quarter HL early in postflexion stage (Table 1). As smallest spines begin to disappear, remaining spines usually form three groups, with 1 or 2 anteriorly on lower preopercular margin, largest spine at angle, and 1 or 2 near upper end of preopercle. Late in postflexion stage spines become shorter and blunter, and numbers of spines near ends of preopercle reduced to 0–1.

First small tooth present near mesial end of each

Table 1. Summary of measurements of *Enchelyurus ater*, expressed as percentage of body length (BL) or head length (HL). For each measurement the mean is given above and the range is given below. For eye diameter, eye length is given first and eye height is given second. N = number of specimens. Notochord flexion occurs within the 4.1–5.0 and 5.1–6.0 mm size categories.

BL (mm)	N	PAL/BL	BD/BL	HL/BL	P ₁ L/BL	P ₂ L/BL	HW/HL	SnL/HL	ED/HL	PSL/HL
2.1–3.0	21	36 32–40	20 17–27	23 19–27	8 7–10	0 0–0	96 82–115	14 8–21	52,44 46–62, 37–54	8 3–12
3.1–4.0	29	34 31–40	17 15–22	23 20–28	8 7–10	0 0–0	75 69–97	17 9–25	42,37 41–53, 32–47	9 6–15
4.1–5.0	24	37 34–40	20 18–23	25 21–29	10 7–16	0.1 0–1	79 69–98	20 17–27	42,41 38–52, 37–45	16 10–24
5.1–6.0	12	38 37–40	21 19–23	25 22–28	12 9–15	1 1–3	76 71–83	21 18–27	42,42 35–45, 35–45	21 16–26
6.1–7.0	2	40 39–40	23 23–24	26 24–27	16 15–16	3 2–3	81 81–82	19 18–20	45,44 43–46, 42–46	27 26–28
7.1–8.0	5	40 38–42	23 22–24	25 25–26	17 13–19	8 6–10	76 72–81	16 14–17	45,45 44–47, 44–47	24 22–26
8.1–9.0	7	39 32–42	22 17–25	25 23–28	17 13–19	9 2–11	75 69–80	16 13–17	44,44 40–48, 40–48	21 19–23
11.1–12.0	1	41	21	25	16	16	68	17	35	15

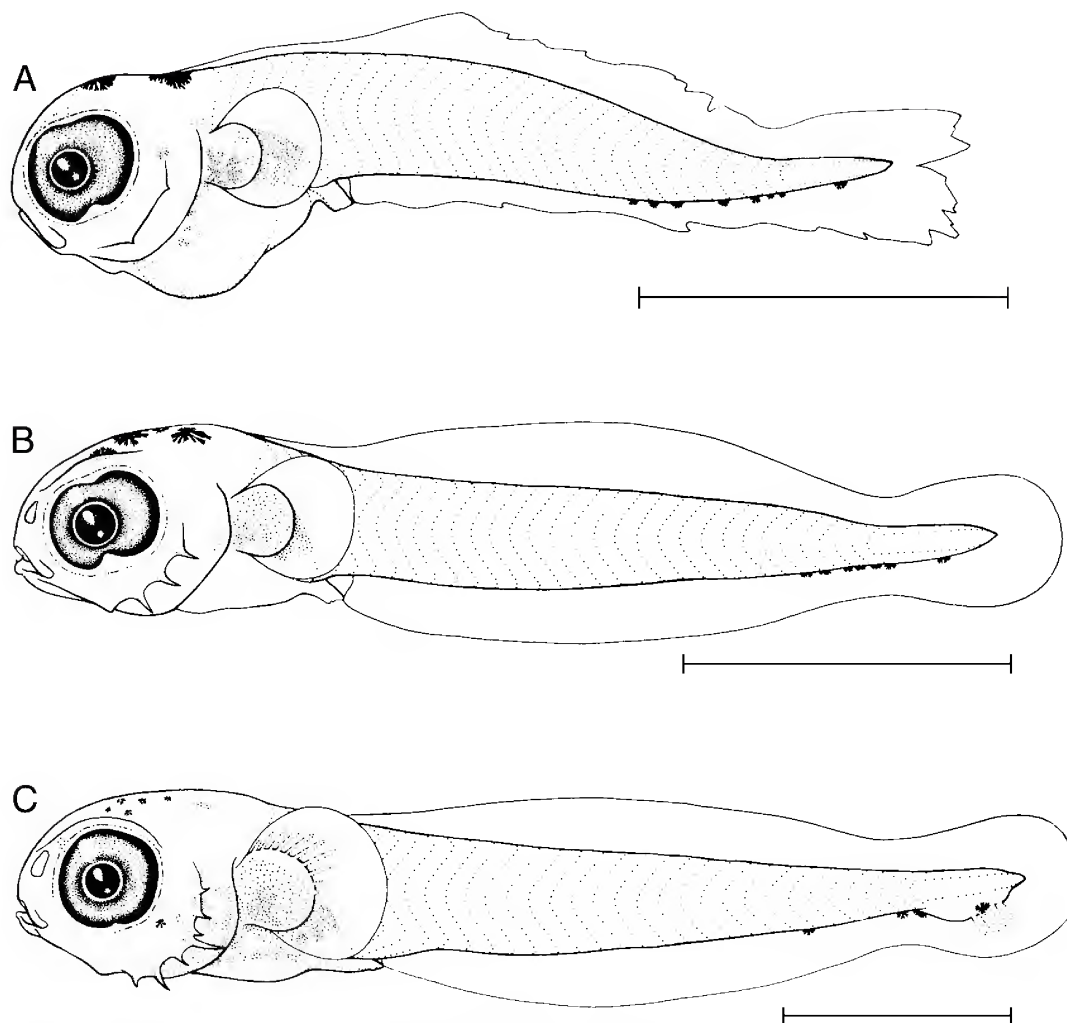


Figure 1 (part). *Enchelyurus ater*, lateral view. A, 2.4 mm (I.29084-001). B, 3.0 mm (I.29099-001). C, 4.4 mm (I.29098-001). D–F, see opposite. Scale bars = 1 mm.

premaxillary bone at 3.1 mm. Second premaxillary tooth added by 4.3 mm and third by 5.6 mm. First lateral premaxillary tooth develops near 8 mm, is larger than anterior teeth and separated from them by an edentulous gap. In largest larva 7 teeth present on each premaxillary bone: 5 anterior and 2 lateral. Anterior teeth have flattened adult form in this specimen.

Dentary teeth appear at about 3.7 mm: a small tooth present near symphysis and larger tooth located anterolaterally on short dorsal process of each dentary bone. Second small anterior tooth added by 4.3 mm and small anterolateral tooth added just posterior to dorsal process between 5–6 mm. In largest larva 6–7 teeth present on each dentary: 5 flattened, adult-type anterior teeth, large anterolateral tooth, and another, smaller lateral tooth on left side.

Frontal bones become ornamented with small spinules by about 4.1 mm and parietal and lower parts of preopercular, articular and dentary bones follow suit by 4.8 mm. Spinules persist through early postflexion stage, then become smaller and more rounded. By about 7 mm they are reduced to low ripples and small bumps.

Fin development. Smallest larvae have broad dorsal, anal and caudal finfolds and pectoral fan, but no preanal finfold or rays forming in any fin. Pectoral-fin rays begin forming first, by about 2.9 mm. Addition of rays is ventrad from uppermost two rays. Full complement of 14–16 rays (usually 15, rarely 16) completed late in flexion stage, by 5.3 mm (Table 2).

Principal caudal-fin rays second to begin forming, late in preflexion stage, and full complement of 7+6 rays present by late flexion stage. Procurrent caudal-fin rays form early in postflexion stage and full complement of 6–8+6–8 rays attained by about 8 mm. Procurrent rays added anteriorly from posteriormost ray.

Dorsal- and anal-fin anlagen form during preflexion stage, beginning at about 4.2 mm. Segmented rays form in both fins beginning at about mid-flexion; anal-fin rays apparently start forming slightly sooner than dorsal-fin rays. Anterior several segmented rays may form simultaneously within each fin and addition of rays is posteriorly in both fins. Full complements of 20–24 segmented dorsal-fin rays (usually 20–21) and 18–23 segmented anal-fin rays (usually 19–21) completed in postflexion stage by about 6.8 mm

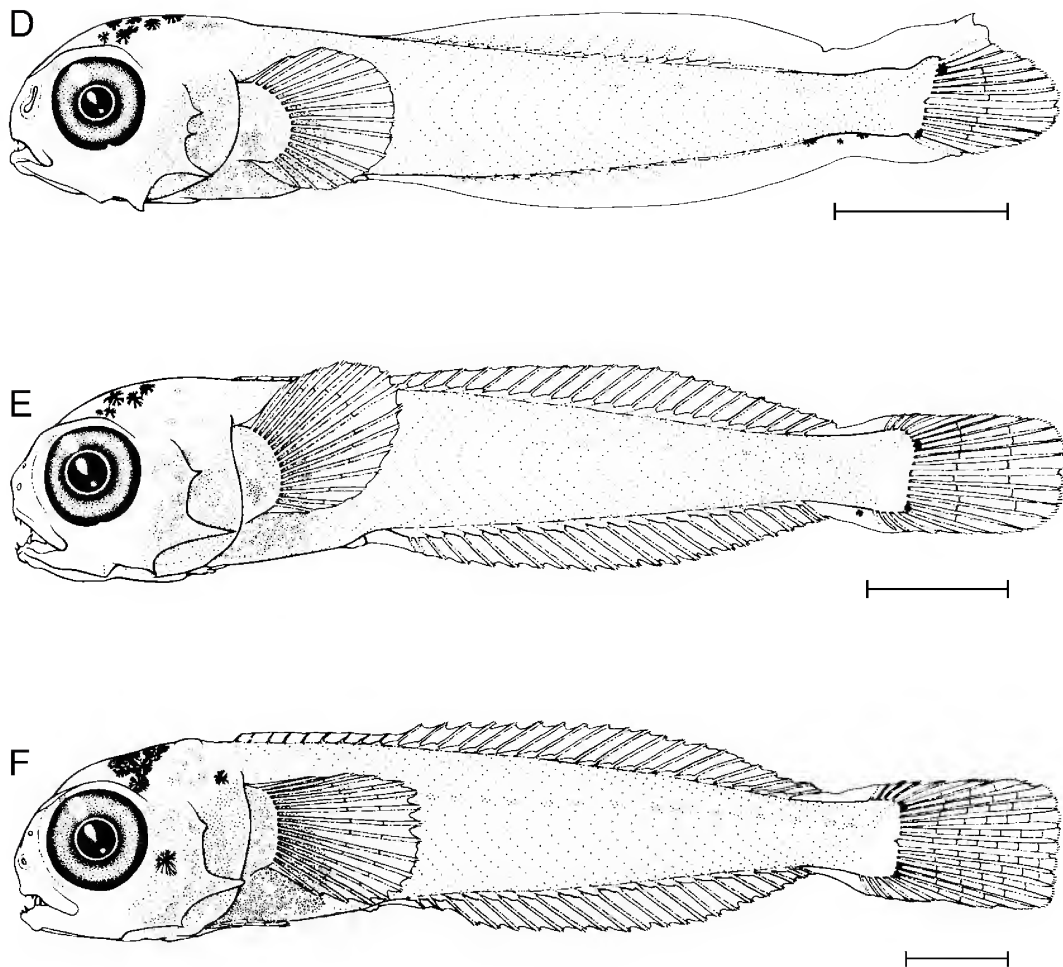


Figure 1 (continued). *Enchelyurus ater*, lateral view. D, 5.4 mm (I.29099-001). E, 6.3 mm (I.29098-001). F, 8.6 mm (I.29098-001). Scale bars = 1 mm.

(Table 2). Anal-fin spines may form simultaneously in postflexion stage; both present by 6.8 mm. Dorsal-fin spines begin to form early in postflexion stage, by about 5.9 mm. Posterior 3 spines may form simultaneously and addition is cephalad, with full complement of 8–10 (usually 9) attained by about 8 mm.

Pelvic-fin buds develop in preflexion stage by about 4.2 mm, and fin rays form early in postflexion stage, by 5.9 mm. Pelvic-fin spine forms by about 8 mm.

Pigmentation. Larvae lightly pigmented, except on head and gut. Head pigmentation initially consists of 1 or 2 pairs of large melanophores posteriorly over midbrain and none to few smaller melanophores more anteriorly over midbrain (Fig. 2), none or 1 anteriorly under forebrain (present in 44% of larvae 3 mm or smaller), and none or 1 just anterior to upper end of preopercle (present in 33% of larvae 3 mm or smaller). Pigmentation over midbrain area gradually increases and area usually covered by flexion stage. Forebrain melanophore usually present after 3 mm (present in about 85% of larvae >3 mm) and after 3.1 mm may spread upward onto anterior margin of forebrain. No other

pigment forms on forebrain area through at least 8.6 mm, but by 11.4 mm a small dorsal melanophore is present above forebrain. Melanophore at upper end of preopercle nearly always present after 3 mm (present in 90% of larvae >3 mm). At about 4 mm melanophores form on inner surface of opercular area, beginning near middle of preopercle, and usually spread to cover much of area by about 6–7 mm. First melanophore on exterior surface of opercular area forms anterior to preopercular angle at about 4.2 mm, but no more than a few more form by 8.6 mm (none in 11.4 mm specimen). A melanophore may form in otic capsule as early as 2.7 mm, but usually capsule is unpigmented until about 4 mm. After 4 mm an epiotic melanophore commonly is present and a prootic melanophore occasionally occurs. Melanophores form on hindbrain during notochord flexion, just after 5 mm. This pigmentation initially consists of only a few dorsal and dorsolateral melanophores, usually only anteriorly, and gradually increases and spreads to cover much of hindbrain by about 8 mm. Melanophores form on ceratohyals after 6 mm, and nearly cover them after about 8 mm.

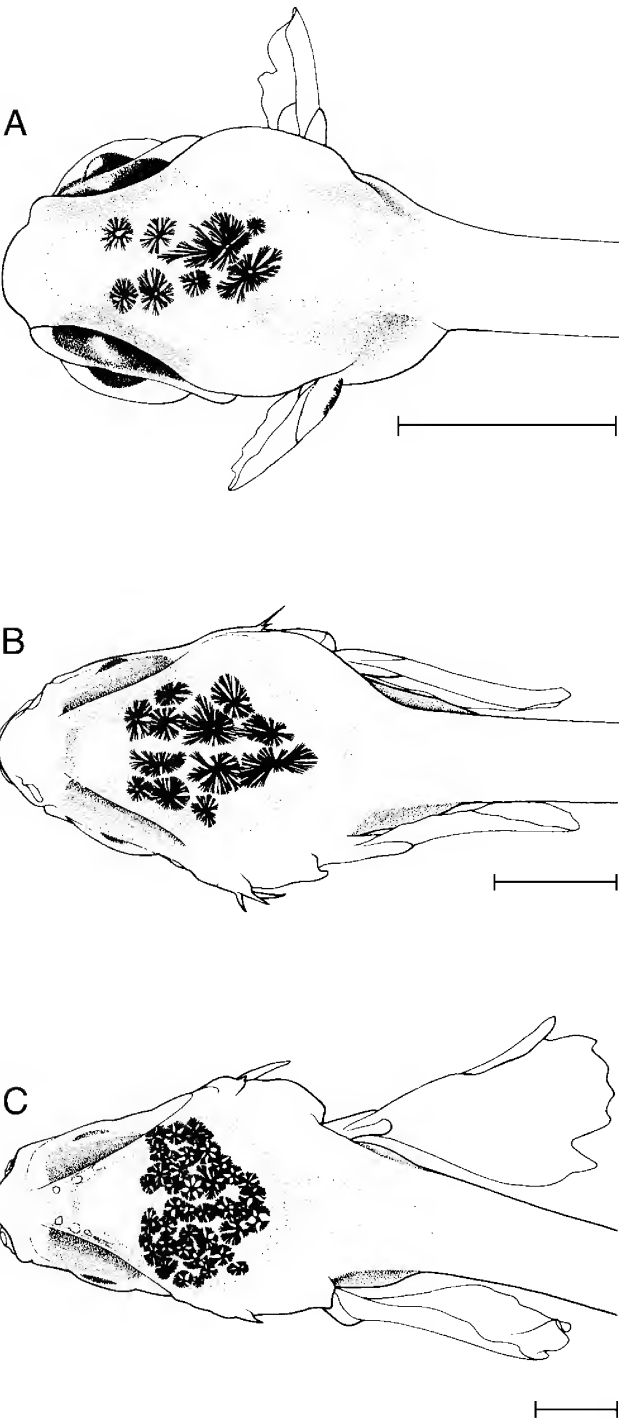


Figure 2. *Enchelyurus ater*, dorsal view of head. A, 3.0 mm (I.29099-001). B, 5.4 mm (I.29099-001). C, 8.6 mm (I.29098-001). Scale bars = 0.5 mm.

A melanophore, often large, is located proximally on lower mesial surface of pectoral base in all larvae except 11.4 mm specimen; there is no other pectoral pigment. A melanophore forms on cleithrum at level of pectoral-fin insertion by 2.6 mm, and others gradually added ventrally

Table 2. Fin-ray counts of larval *Enchelyurus ater*. Abbreviations for larval stages are: Pr = preflexion; F = flexion; Po = postflexion. Cpri = principal caudal-fin rays; Cpro = procurent caudal-fin rays; body length (BL) in mm.

BL	stage	D	A	P ₁	P ₂	Cpri	Cpro
2.3	Pr	0	0	0	0	0	0
2.9	Pr	0	0	2	0	0	0
3.0	Pr	0	0	0	0	0	0
3.6	Pr	0	0	4	0	0	0
4.4	Pr	0	0	10	0	2+2	0
4.4	Pr	0	0	11	0	2+2	0
4.8	F	0	8	14	0	5+5	0
5.3	F	17	16	15	2	7+6	0
5.4	F	15	14	14	0	6+6	0
5.4	F	16	14	15	0	7+6	0
5.7	Po	18	17	15	0	7+6	2+2
5.9	Po	III,20	19	15	2	7+6	1+1
6.8	Po	III,20	II,19	16	2	7+6	5+5
8.0	Po	IX,21	II,19	15	I,2	7+6	7+6
8.1	Po	IX,21	II,18	15	I,2	7+6	7+7
8.6	Po	IX,22	II,20	15	I,2	7+6	7+7
11.4	Po	IX,22	II,19	15	I,2	7+6	8+8

along cleithrum, eventually forming a series along most of its length below pectoral-fin origin. Pelvic fins unpigmented.

Gut pigmentation initially largely limited to dorsum, except terminal section of hindgut is unpigmented. Melanophores spread ventrolaterally, covering upper 50–60% of gut before 3 mm and reaching ventrum by about 4.5 mm. One or two melanophores may be present anteroventrally on or near longitudinal midline in preflexion stage (present in 20%), but more commonly no ventral pigment on gut until flexion stage, when melanophores spread over ventrum from each side, meeting along longitudinal midline near end of stage (by 5.6 mm). Pigmentation on gut becomes dense during flexion and postflexion stages, except often sparser midlaterally, especially behind pectoral-fin bases, and in late flexion stage, along ventral midline. Melanophores in these sparsely pigmented areas often smaller than those in adjacent areas. During postflexion stage gut pigmentation may become noticeably denser in ventrolateral band along each side.

Postanal pigmentation initially consists of 2–9 (usually 3–6) melanophores more or less evenly spaced along ventral margin of last 3–11 (modally 6) myomeres plus 1–2 melanophores (usually 1) ventrally on notochord tip. Anterior melanophores disappear during flexion and early postflexion stages; thereafter none, or only posterior 1–3, remain. Remaining melanophore(s) may be on ventral margin, shallowly internal, or on caudal finfold near body margin.

Specimens ≤4 mm usually have single ventral melanophore near middle of notochord tip; after 4 mm there usually are 2 located proximally and distally on notochord tip. These

become located at margins of lower and upper hypural plates, respectively, as caudal fin develops.

Internal dorsal melanophore series forms posteriorly over notochord during flexion stage and spreads cephalad to full length of vertebral column by about 7.6–8.6 mm, but becomes increasingly difficult to see as melanophores are obscured by overlying tissue in larger larvae. Melanophores over abdominal vertebrae typically are more widely spaced than those over caudal vertebrae.

***Enchelyurus kraussi* (Klunzinger, 1871)**

Figs. 3, 4

Morphology. Smallest specimen (1.6 mm) has pigmented eyes, open mouth, a small preopercular spine, remnant of yolk sac, and probably had hatched not long before collection. Notochord flexion begins at about 4.3–4.8 mm, is completed by 5.5 mm. Most advanced larvae (11.5 and 14.5 mm) approaching settlement stage as shown by resorption of preopercular spines (incomplete), presence of adult-type teeth, and development of cephalic sensory pores. Springer (1972) listed an 11.4 mm juvenile (presumably settled) from the Seychelles Islands and Kubo & Sasaki (2000) described a pelagic, transforming specimen 12.9 mm from Japan. Size at transformation and settlement are unknown for eastern Australian *E. kraussi*, but probably are in the vicinity of 14–15 mm.

Head initially rounded and broad, gut short and coiled, tail elongate and compressed. During preflexion stage larvae become more slender as yolk consumed, then gradually become deeper-bodied and more compressed with slightly larger head and longer preanal length (Table 3). These dimensions change little thereafter, except relative preanal length increases slowly until late postflexion stage. Eyes initially large and oval to

somewhat rectangular (elongate horizontally), becoming round between 3.4–3.9 mm. Snout moderately short, rounded, changes little. There are 33–35 myomeres (usually 34): 6–7 preanal plus 26–28 postanal through preflexion stage, shifting to 10 preanal plus 24 postanal by late postflexion stage (c. 11 mm).

Smallest specimen has 1 small spine on posterior preopercular margin (present only on right side). By 3.1 mm 3 spines present: one each near lower and upper ends of preopercle and another at angle. Maximum of 6–7 spines attained by 3.9 mm. When more than 3 spines present, arrangement is variable, with 1–3 spines along lower preopercular margin, single spine at the angle, and 1–3 along upper margin. Bilateral asymmetry in number of spines apparently uncommon: only 2 specimens had 1 more spine on one side than on other. As larvae grow, smaller preopercular spines are overgrown or resorbed: by midflexion (4.8 mm) only 3 remain and by mid-postflexion (c. 8 mm) only spine at angle remains. Early in preflexion stage spines are of similar length; the spine nearest each end of preopercle typically is slightly longer than other(s). These remain longest until about 4 mm when they are overtaken by spine at angle, which reaches a maximum of just over one-quarter HL by mid-postflexion stage (Table 3). Spine gradually resorbed near end of pelagic larval phase. In largest specimen (14.5 mm) resorption incomplete and spine remains short and blunt.

No teeth visible in 1.6 mm specimen and none visible on premaxillae in any preflexion stage specimen. A small conical tooth first visible near mesial end of each premaxilla in 4.8 mm midflexion specimen, and by end of stage another has been added on each side of this tooth. By mid-postflexion stage each premaxilla bears 5–6 teeth anteriorly, separated by an edentulous gap from 1 or 2 larger anterolateral teeth (when 2 present, anterior tooth usually largest). Anterior, conical larval teeth may

Table 3. Summary of measurements of *Enchelyurus kraussi*, expressed as percentage of body length (BL) or head length (HL). For each measurement the mean is given above and the range is given below. For eye diameter, eye length is given first and eye height is given second (by 5 mm BL the eyes are round and only eye length is given). N = number of specimens measured. The specimen in the 5.1–6.0 mm size class is undergoing notochord flexion.

BL (mm)	N	PAL/BL	BD/BL	HL/BL	P ₁ L/BL	P ₂ L/BL	HW/HL	SnL/HL	ED/HL	PSL/HL
1.6–2.0	2	38	22	24	11	0	105	14	49,43	7
		37–39	20–24	22–25	(N=1)	0–0	105–105	12–16	49–50, 41–45	5–9
3.1–4.0	9	35	18	23	8	0	85	19	40,37	10
		32–38	16–21	20–26	6–10	0–0	79–92	12–21	37–47, 31–41	5–13
4.1–5.0	3	37	19	24	10	<0.1	82	18	39,37	18
		36–37	19–20	23–25	10–11	0–0.2	77–90	16–21	37–40, 36–38	12–24
5.1–6.0	1	38	24	27	15	2	70	19	38	22
8.1–9.0	2	38	24	26	18	10	79	18	38	27
		38–39	23–26	25–28	17–19	8–11	79–80	17–20	37–38	27–28
11.1–12.0	4	44	24	26	19	17	73	16	36	13
		42–47	23–24	25–27	18–20	15–18	62–80	15–19	35–36	8–20
12.1–13.0	3	42	24	27	20	17	72	17	33	11
		41–43	24–24	26–28	19–21	16–18	71–72	16–18	33–34	7–13
14.1–15.0	1	41	22	24	19	16	79	19	34	9

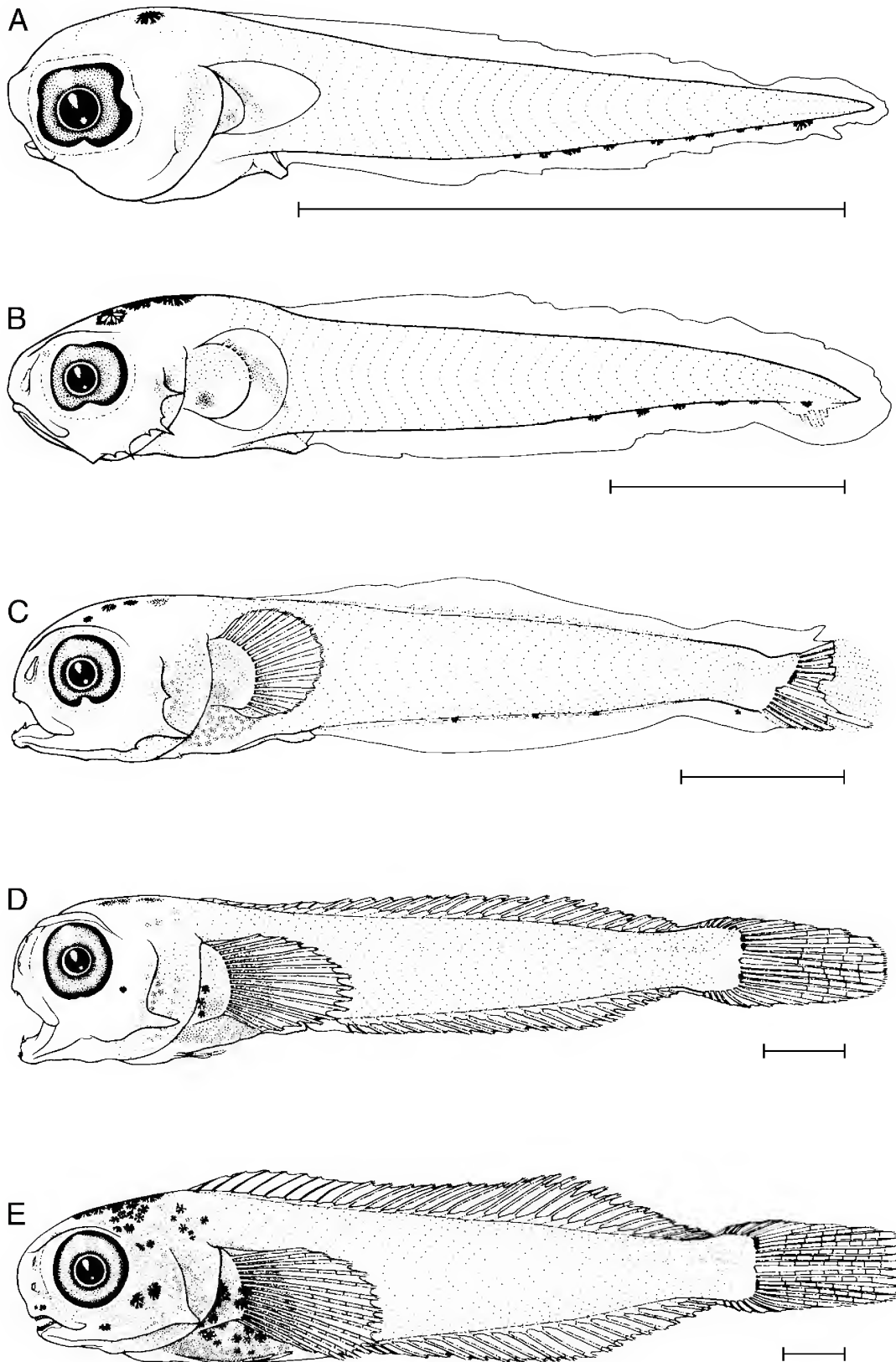


Figure 3. *Enchelyurus kraussi*, lateral view. A, 1.6 mm, preopercular spine present only on right side in this specimen, but shown as if it were present on the left (I.30852-006). B, 3.7 mm (I.39541-001). C, 4.8 mm (I.39210-001). D, 8.6 mm (I.21758-003); E, 11.5 mm (I.21754-009). Scale bars = 1 mm.

broaden into flattened adult form. By c. 11 mm all 5–9 anterior teeth are adult form and through 14.5 mm no premaxillary teeth added.

Dentary teeth first visible at 3.2 mm: each dentary bears a small, conical, anterior tooth near its mesial end and another, slightly larger, anterolaterally. Anterolateral tooth is attached to short dorsal process of dentary bone. No dentary teeth added through at least midflexion, but by end of stage another 2 small, conical teeth are present anteriorly. By mid-postflexion stage anterior teeth all acquiring adult form, anterolateral tooth is moderately large, and a small tooth is added just posterior to dorsal process. Occasionally, both lateral teeth are large on one or both dentaries. The 5–8 anterior teeth are separated by a short, edentulous gap from lateral teeth.

Frontal bones become slightly rugose at about 3.9 mm and by 4.2 mm both they and posteroventral parts of dentary bones are ornamented with small spinules. Spinules increase in density on frontals and dentaries and form on angular, articular, parietal and preopercular bones, including preopercular spines, during notochord flexion. Ornamentation persists through at least 14.5 mm, but smooths to low ripples and small bumps by 11.2 mm.

Fin development. Smallest specimen has dorsal, anal and caudal finfolds and pectoral fan, but lacks preanal finfold. Upper 2–3 pectoral-fin rays forming by 3.1 mm (Table 4); rays added ventrad. Full complement of 14–16 (usually 15) rays present by early postflexion stage (5.5 mm).

Principal caudal-fin rays next to begin forming, by about 3.6 mm. Addition of rays is anteriorly (= ventrally) and posteriorly (= dorsally) from central rays; full complement of 7+6 rays present by beginning of postflexion stage, when procurrent rays begin forming. Procurrent rays added anteriorly from posteriormost ray and full complement of 6–7+6–7 rays present by 8.7 mm.

Dorsal- and anal-fin anlagen form late in preflexion stage, by about 4.2 mm, and segmented fin-rays begin to form during flexion stage. Location and number of these first rays, direction(s) of initial addition of rays, and whether initial ray formation is simultaneous in both fins could not be determined. Last few segmented rays added caudad in each fin during early postflexion stage. Full complements of 21–24 segmented dorsal-fin rays (modally 22 rays), 18–20 segmented anal-fin rays (modally 19 rays) present by 8.7 mm. First dorsal-fin spines form early in postflexion stage (c. 5.5 mm). Posterior 3 spines may form simultaneously and addition is cephalad. Full complement of 7–9 spines (modally 8 spines in eastern Australian waters) present by 8.7 mm.

Pelvic-fin buds form late in preflexion stage, by 4.2 mm, and segmented rays first appear at beginning of postflexion stage. Full complement of 1 spine and 2 segmented rays present by 8.7 mm.

Pigmentation. Larvae lightly pigmented, except on head and gut. Head pigmentation initially consists of pair of large, dorsal melanophores posteriorly near midline of midbrain, few additional melanophores scattered more anteriorly over midbrain, usually a small melanophore internally at anterior margin of forebrain (none in 1.6 and 3.1 mm specimens), and usually 1–2 melanophores on inner surface near centre

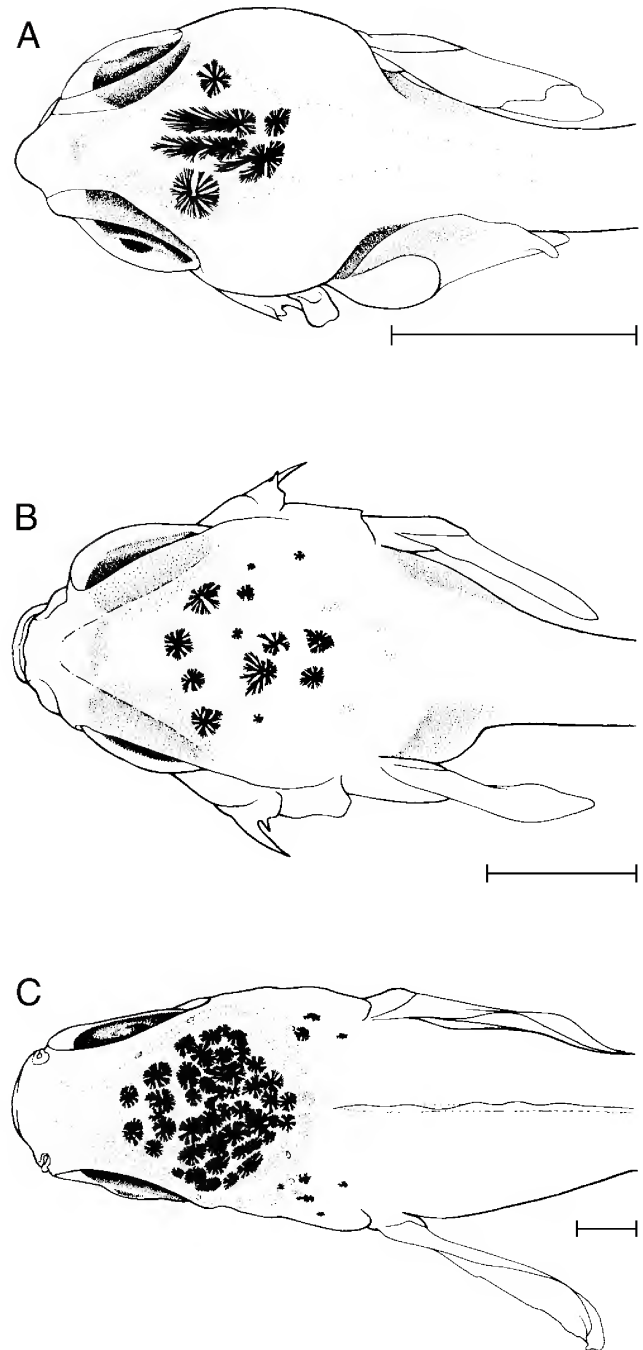


Figure 4. *Enchelyurus kraussi*, dorsal view of head. A, 3.3 mm (I.39210-002). B, 4.8 mm (I.39210-001). C, 11.5 mm (I.21754-009). Scale bars = 0.5 mm.

of opercular area (Figs. 3B, 4A). Dorsal pigmentation over midbrain area increases, completely covering it between late preflexion and early postflexion stage, and usually spreads forward over forebrain area early in postflexion stage (by 5.5 mm; occasionally absent in larvae as large as 11.5 mm). Melanophores usually form anteriorly on upper jaw and internally in ethmoid region at about 11.5 mm

(absent in both areas in 12.3 mm specimen). Forebrain pigmentation unchanged until late postflexion stage (c. 11.5 mm) when few scattered melanophores are added. One to three melanophores form in otic capsule early in preflexion stage, by about 3.2 mm. Melanophores form on hindbrain early in postflexion stage and usually cover it (sparsely) by about 8.7 mm. External melanophores form on nape late in postflexion stage (c. 11.5–12 mm). Opercular pigmentation unchanged until early postflexion stage when melanophores form patch on central mesial surface, then spread to cover much of area and extend onto branchiostegal membranes by about 12 mm. Melanophores may form on mesial surface of ceratohyal, primarily near ceratohyal-interhyal articulation, between 11.5–14.5 mm (present in 3 of 7 specimens in this size range). External melanophore forms below eye, just anterior to preopercular angle, by 8.6 mm, and is joined at about 14.5 mm by one just below mid-eye and another just below anterior margin of eye.

Lower, proximal part of mesial surface of pectoral-fin base always is pigmented. Through mid-postflexion stage this pigment usually is 1 large melanophore (occasionally 2, 4 covering entire mesial surface in one specimen), but by 11.2 mm more melanophores are added, covering lower half of mesial surface. Melanophores form on outer surface by 8.6 mm. These initially are proximal, on lower half of base, and spread to cover much of lower half by 11.2 mm. Melanophores usually form on pectoral-fin rays at about 11.5 mm: 1 or 2 are located near bases of 1 or 2 of lower 8 rays. Melanophore forms on cleithrum at level of pectoral-fin insertion between 2.0–3.2 mm and more are added, first ventrad, then both ventrad and dorsad, forming a series along cleithrum from pectoral origin to near cleithral symphysis by end of preflexion stage.

Gut pigmentation initially is only dorsal (except terminal section of hindgut always is unpigmented). Ventral pigment occasionally is present in small preflexion stage larvae: 3.1 mm specimen has a small ventral melanophore at anterior centre of gut. Melanophores spread ventrad from dorsum during preflexion stage, beginning anteriorly and reaching ventrum by c. 4.2 mm, then completely encircle gut by mid-flexion. External melanophores form on abdominal area between 8.7–11.5 mm but remain sparse (absent in some) through at least 14.5 mm.

Postanal pigmentation initially limited to ventral margin of tail. Through most of preflexion stage 4–14 melanophores are arrayed irregularly along last 2–20 myomeres and notochord tip. Usually, spacing between first 2–3 melanophores in series is wider than that between more posterior melanophores. Last (or last 2) melanophore(s) in series nearly always located on notochord tip and becomes located on margin(s) of one (or both) hypural plates late in preflexion stage. Postflexion stage larvae nearly always have an elongate melanophore at distal margin of each hypural plate (sometimes 2 on upper plate). Ventral melanophores decrease in number after about 4 mm and by postflexion stage there are none. Internal melanophores form over notochord during postflexion stage, extending to full length by 8.6 mm, but are difficult to see anteriorly.

Table 4. Fin-ray counts of larval *Enchelyurus kraussi*. Abbreviations for larval stages are: Pr = preflexion; F = flexion; Po = postflexion. Cpri = principal caudal-fin rays; Cpro = procurent caudal-fin rays; body length (BL) in mm.

BL	stage	D	A	P ₁	P ₂	Cpri	Cpro
1.6	Pr	0	0	0	0	0	0
3.1	Pr	0	0	2	0	0	0
3.2	Pr	0	0	4	0	0	0
3.3	Pr	0	0	4	0	0	0
3.4	Pr	0	0	3	0	0	0
3.6	Pr	0	0	7	0	2+2	0
3.7	Pr	0	0	8	0	2+2	0
3.9	Pr	0	0	7	0	0	0
4.2	Pr	0	0	12	0	3+3	0
4.8	F	12	12	14	0	7+6	0
5.5	Po	III,21	I,18	15	2	7+6	1+1
8.6	Po	VIII,21	II,19	15	I,2	7+6	6+6
11.2	Po	VIII,22	II,19	15	I,2	7+6	7+7
11.5	Po	VIII,23	II,20	15	I,2	7+6	6+6
14.5	Po	VIII,22	II,20	15	I,2	7+6	6+6

Comparisons

Larval *Enchelyurus ater* from the Tuamotu Archipelago, *E. brunneolus*, and eastern Australian *E. kraussi* closely resemble one another in most characters, but each is distinguishable by small differences in several characters. Among the 48 characters examined, *E. ater* and *E. brunneolus* are similar to one another, and both are different from *E. kraussi*, in eight or nine (Table 5: characters 3, 4, 13, 17, 19, 30, 32, probably 12; Tables 1, 3, 6: eye diameter), and *E. ater* is similar to *E. kraussi* (both different from *E. brunneolus*) in four (Table 5: characters 18, 25, 31; Tables 1, 3, 6: pectoral-fin length).

Enchelyurus ater and *E. brunneolus* both apparently acquire the first premaxillary teeth (character 4) earlier in development, and both probably settle from the plankton (3) at a smaller size than does *E. kraussi*. (Settlement size is unknown for *E. ater* and *E. kraussi*, but comparison of the developmental states of the largest larvae with similarly developed *E. brunneolus* suggests that *E. ater* and *E. brunneolus* settle at about the same size, and that *E. kraussi* settles at a larger size, at least in eastern Australian waters.) Both *E. ater* and *E. brunneolus* acquire ceratohyal pigmentation (30) beginning at about 6–7 mm, while *E. kraussi* develops it much later, at 11.5 mm or larger. This pigmentation typically is more extensive in *E. ater* than in the other two.

On the other hand, neither *E. ater* nor *E. brunneolus* develop dorsal pigmentation over the forebrain (19) as early as *E. kraussi*, and both usually retain the early oval to rectangular eye shape (13) somewhat longer. *Enchelyurus kraussi* has smaller eyes relative to head length than either of the other two, both of which have similar relative eye

Table 5. Comparison of characters in larval *Enchelyurus ater*, *E. brunneolus* and *E. kraussi*.

character	<i>E. ater</i>	<i>E. brunneolus</i>	<i>E. kraussi</i>
approximate size (mm) at:			
1 hatching	2.3	2.2	1.6
2 flexion	5.0–5.5	4.5–5.5	4.5–5.5
3 settlement	probably ~12	<12	probably ~15
4 first premaxillary teeth	3.1	2.9	4.8
5 first dentary teeth	3.7	3.6	3.2
6 first pectoral-fin rays	2.9	<3.2	≤3.1
7 first caudal-fin rays	4.4	4.0	4.2
8 first anal-fin rays	>4.4, <4.8	5.2	>4.2, <4.8
9 first dorsal-fin rays	>4.8, <5.3	5.2	4.8
10 first dorsal-fin spines	5.9	5.6	5.5
11 first pelvic-fin rays	5.9	5.5	5.5
12 single preopercular spine	>11.4	10	8
13 eyes round	4.4–5.0	4.5	3.4–3.9
number of myomeres:			
14 preflexion	6–7+27–28	7+28	6–7+26–28
15 postflexion	9–10+24–26	8–9+25–27	10+24
16 max. no. preopercular spines	6–7	6–7	6–7
17 preopercular ornamentation	lower half	usually only lower half	full length
melanophores on/in:			
18 forebrain, anterior margin	usually (+) by 3.3 mm	usually (-) before 9.3 mm	usually (+) by 3 mm
19 forebrain, dorsal	(-) through 8.6 mm	(-) before 9.3 mm	usually (+) by 5.5 mm
20 forebrain, ventral	(-) through 11.4 mm	(-)	(-)
21 midbrain, dorsal	(+)	(+)	(+)
22 midbrain, lateral	(-) through 8.6 mm	usually (-) before 7.2 mm	(-)
23 midbrain, ventral	(-) through 8.6 mm	(-)	(-)
24 hindbrain, dorsal	(+) by 5.4 mm	usually (+) by 5.8 mm	(+) by 4.8 mm
25 hindbrain, lateral	(-) before 6.0 mm	usually (+) by 4.2 mm	(-) before 8.6 mm
26 hindbrain, ventral	(-) through 8.6 mm	(-)	(-)
27 otic capsule	usually 1–2	1–2	1–3
28 roof of mouth/ethmoid area	(-) through 8.6 mm	usually (+) by 8.8 mm	usually (+) by 11.5 mm
29 pharyngobranchial	(+)	(+)	(+) by 3.3 mm
30 ceratohyal	(+) after 6 mm	(+) after ~7 mm	(+) by 11.5 mm in some
31 pectoral-fin base	(+), inner surface	(-)	(+), inner surface; (+), outer surface by 8.6 mm
32 pectoral-fin rays	(-) through 8.6 mm	(-)	(+) by 11.5 mm
33a gut, preflexion stage	dorsal	dorsal	dorsal
33b gut, postflexion stage	unevenly covered, often denser ventrolateral band	usually ~evenly covered, denser ventrolateral band in some	~evenly covered
ventral margin of tail:			
34a preflexion: range (mode)	3–11 (6)	2–10 (5)	4–14 (8,9,13)
34b postflexion: range (mode)	0–3 (1,2)	0–2 (0)	0 (0)

size through about 7 mm (cf. Tables 1, 3, 6). *Enchelyurus kraussi* also may differ from the other two species in the larval length at which the number of preopercular spines is reduced to one (12), although the incomplete series of *E. ater* makes this character difficult to assess. In *E. kraussi* only the

large spine at the angle remains by about 8 mm—well before settlement. In *E. brunneolus* this process is complete by about 10 mm—shortly before settlement. In the largest *E. ater* (11.4 mm) the process is underway but incomplete, suggesting that here too it is finished shortly before settlement. These characters

Table 6. Summary of measurements of *Enchelyurus brunneolus*, expressed as percentage of body length (BL) or head length (HL). For each measurement the mean is given above and the range is given below. N = number of specimens. Notochord flexion occurs within the 4.1–5.0 and 5.1–6.0 mm size classes.

BL (mm)	N	PAL/BL	BD/BL	HL/BL	P ₁ L/BL	SnL/HL	ED/HL	PrSL/HL
2.1–3.0	18	38 33–41	19 18–28	23 19–27	10 5–13	10 6–14	51 44–60	6 0–11
3.1–4.0	11	38 32–46	19 16–21	23 19–28	11 8–16	18 10–25	46 38–53	9 5–14
4.1–5.0	6	40 36–47	20 17–23	25 23–27	14 10–17	20 17–23	39 33–41	17 11–21
5.1–6.0	4	44 39–48	23 22–24	28 22–31	20 12–27	18 15–21	41 38–44	22 20–26
6.1–7.0	2	43 42–44	24 22–26	25 23–26	20 20–20	17 16–18	44 43–45	23 20–25
7.1–8.0	2	40 40–40	22 22–22	27 26–28	25 24–26	14 14–15	40 38–42	24 22–25
8.1–9.0	3	42 39–46	22 20–24	26 24–29	25 23–28	15 13–18	40 38–43	20 16–24
9.1–10.0	1	40	21	25	24	17	41	17
10.1–11.0	2	44 44–44	22 21–23	27 27–27	27 26–27	15 13–17	36 35–37	2 0–4
11.1–12.0	11	44 43–48	22 20–24	26 24–28	25 22–26	16 11–19	38 36–41	2 0–7
12.1–13.0	1	41	19	25	27	15	39	0

suggest prolonged retention of an early developmental state in larval *E. ater* and *E. brunneolus*.

Larval *E. kraussi* develop preopercular ornamentation (17) in the form of small spinules and ripples extending the full length of the preopercle and out onto the spine at the angle during the flexion and postflexion stages (Fig. 5C). Larval *E. ater* and *E. brunneolus* acquire similar ornamentation, but it is restricted to the lower part of the preopercle in *E. ater* and usually occurs only on the lower part in *E. brunneolus* (Fig. 5A,B), although an occasional specimen also has small patches of spinules around the bases of some of the upper preopercular spines. This might be considered a gradient in the extent of preopercular ornamentation: *kraussi* > *brunneolus* > *ater*; however, because the upper preopercular ornamentation is uncommon in *E. brunneolus* it seems preferable to consider *E. ater* and *E. brunneolus* similar, and both different from *E. kraussi*, in this character. Ornamentation of this sort on any or all of the dentary, articular, angular, and preopercular bones may be a specialization of the Omobranchini, perhaps more extensively developed in *Enchelyurus* (at least in this species group) than in *Omobranchus*.

Characters in which larval *E. ater* resemble *E. kraussi* (and both differ from *E. brunneolus*) include the size at which melanophores form at the anterior margin of the forebrain (18) and laterally on the hindbrain (25), pigmentation of the pectoral-fin base (31), and relative pectoral-fin length (Tables 1, 3, 6). Both *E. ater* and *E.*

kraussi acquire the anterior forebrain melanophore early in the preflexion stage: it is present in 44% of *E. ater* smaller than 3 mm and in 85% of larger specimens. Respective values for *E. kraussi* are 33% for larvae smaller than 3.2 mm and 100% for larger specimens. *Enchelyurus brunneolus* lacks this melanophore in the preflexion stage and rarely has it before about 9 mm, well into the postflexion stage. On the other hand, *E. brunneolus* develops lateral melanophores on the hindbrain early in the flexion stage (by about 4.2 mm), in contrast to during the postflexion stage in *E. ater* (by about 6 mm) and *E. kraussi* (by 8.6 mm).

Pectoral-fin pigmentation is light but nearly always present on the mesial surface of the base (31) in *E. ater* (lacking only in the 11.4 mm specimen) and apparently always is present in *E. kraussi*, in contrast to *E. brunneolus* which has none before late postflexion stage, when a single melanophore may form on the lateral surface of the base near the insertion in some specimens (most commonly the pectoral base is unpigmented before settlement). Larval *E. kraussi* also acquire melanophores on the lateral surface of the pectoral-fin base by 8.6 mm, and in contrast to *E. ater* and *E. brunneolus*, on one or two of the lower fin-rays (32) by 11.5 mm. The degree of pectoral-fin pigmentation thus might be viewed as a gradient: *kraussi* > *ater* > *brunneolus*. Relative pectoral-fin length is similar in *E. ater* and *E. kraussi*, and smaller in both compared with *E. brunneolus*, throughout larval development (Tables 1, 3, 6).

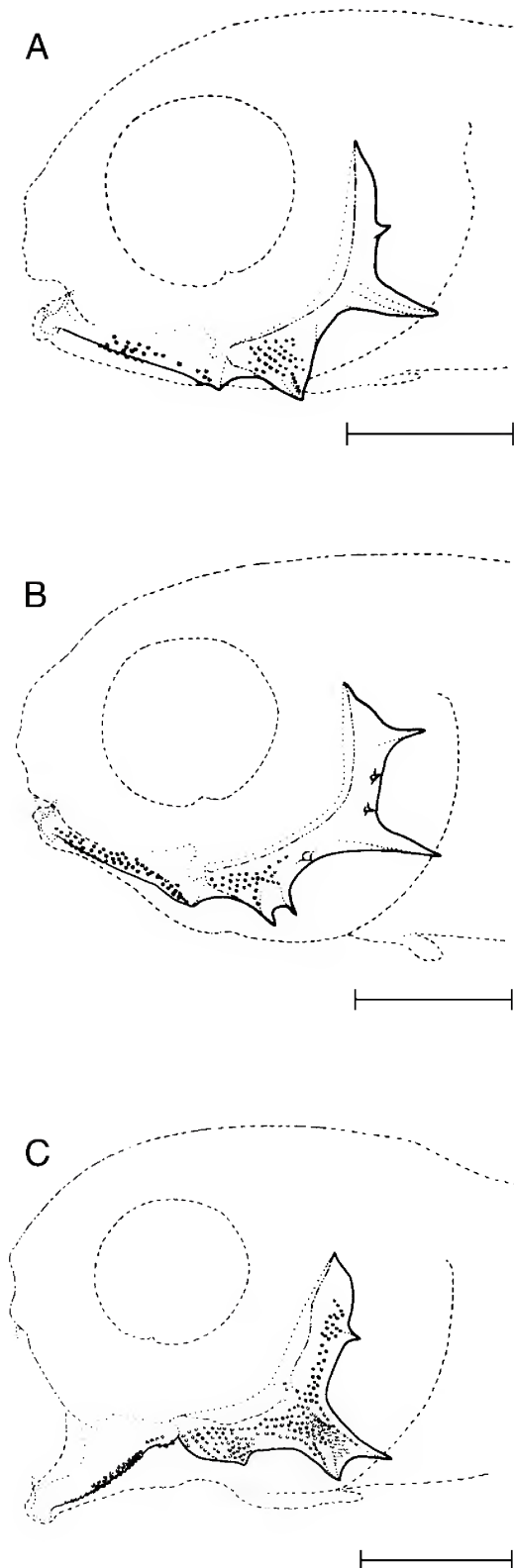


Figure 5. Ornamentation (slightly exaggerated for clarity) of the dentary, articular, angular, and preopercular bones of *Enchelyurus*. A, *E. ater*, 5.4 mm (I.29099-001). B, *E. brunneolus*, 5.9 mm (Kahe Transect Series, VM-3). C, *E. kraussi*, 5.5 mm (I.25131-001), the bifurcate major preopercular spine of this specimen is unusual. Scale bars = 0.5 mm.

Interrelationships

A formal phylogenetic analysis based on the larval characters of *Enchelyurus* was not done. Apart from the three *Enchelyurus* species, larval Omobranchini are known for only a few *Omobranchus* species (Mito, 1966; Visweswara Rao, 1970; Dotsu & Oota, 1973; Springer & Gomon, 1975; Houde *et al.*, 1986; Watson & Miskiewicz, 1998; Kawaguchi *et al.*, 1999). The interrelationships of these two genera are unknown (Springer, 1972) and thus an appropriate outgroup could not be selected. Blenniini has been hypothesised to be the sister group of Omobranchini plus Phenablenniini (whose larvae are unknown) and Nemophini (Springer, 1972; Smith-Vaniz, 1976; Bock & Zander, 1986; Williams, 1990). Among the three blenniini species only the larvae of *Blennius ocellaris* are known (Ford, 1922; Padoa, 1956; Russell, 1976). A cursory attempt was made to polarize the larval characters of *Enchelyurus*, using *B. ocellaris* as an outgroup. This required the assumptions that: 1) larval *Blennius ocellaris* are representative of the other two species of Blenniini; and 2) the characters presumed to be shared among the blenniini are plesiomorphic. Given these assumptions, and the limitations imposed by the level of detail available in the literature descriptions of larval *B. ocellaris*, only three morphological (3, 4, 13) and three pigmentation (18, 19, 31+32) characters (all but one of these, pectoral-fin pigmentation, may be interrelated) could be polarized. Among the morphological characters, *E. ater* and *E. brunneolus* display a presumed apomorphic state in acquiring teeth sooner and retaining an oval eye shape longer in development, and settling from the plankton at a smaller size (settlement size assumed for *E. ater*) than *B. ocellaris*. *Enchelyurus kraussi* is intermediate in that it acquires the round eye shape early like *B. ocellaris*, begins to develop teeth at an earlier stage than *B. ocellaris* but later than the other two *Enchelyurus* species, and probably settles from the plankton at a size smaller than *B. ocellaris* but larger than the others. Among the pigment characters, both *E. ater* and *E. brunneolus* share the presumed apomorphic state of delayed development of dorsal pigment over the forebrain area, in contrast to early development in *B. ocellaris* and *E. kraussi*. The presumed apomorphic state of delayed acquisition of internal forebrain pigment is displayed only by *E. brunneolus*; the other three acquire this pigmentation early in larval development. *Enchelyurus brunneolus* likewise is alone in displaying the presumed apomorphic state of unpigmented pectoral fins, in contrast to the extensively pigmented pectoral fins of *B. ocellaris*. *Enchelyurus ater* and *E. kraussi* display intermediate states, with pigment on the pectoral-fin base in both, and forming on some lower rays in *E. kraussi*.

These tenuous assessments of character polarity are an inadequate basis for demonstrating relationships, but they do suggest a hypothesis of relationships among the three *Enchelyurus* species: *E. ater* is the sister species to *E. brunneolus*, seemingly the most derived species in the group, and *E. kraussi*, perhaps the least derived, is the sister species to the other two.

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The Moray Eels of Australia and New Zealand, with the Description of Two New Species (Anguilliformes: Muraenidae)

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ABSTRACT. Australian and New Zealand moray eel type specimens in museums have been re-examined, their identities established, and brief descriptions of the specimens written. A key to the 59 muraenid species of Australia and New Zealand is presented. Ten species that have remained relatively unknown or inadequately described are redescribed and illustrated: *Gymnothorax annasona* Whitley, 1937; *G. atolli* (Pietschmann, 1935); *G. cribroris* Whitley, 1932a; *G. longinquus* (Whitley, 1948); *G. nubilus* (Richardson, 1848); *G. obesus* (Whitley, 1932a); *G. porphyreus* (Guichenot, 1848); *G. prasinus* (Richardson, 1848); *G. prionodon* Ogilby, 1895; and *G. woodwardi* McCulloch, 1912. A new species from northern Australia is described as *G. cephalospilus*, and one from southern Australia is described as *G. austrinus*. New synonymies are proposed: *Muraena helena australis* Richardson, 1848, and *Muraena vorax* Ogilby, 1907 = *Muraena helena* Linnaeus, 1758; *Muraena euptera* Günther, 1870 = *Gymnothorax nubilus* Richardson, 1848; *Muraena tuhua* Griffin, 1933, and *Gymnothorax griffini* Whitley & Phillipps, 1939 = *Gymnothorax obesus* (Whitley, 1932a); *Gymnothorax maculaepinnis* Bleeker, 1866, and *Gymnothorax leecote* Scott, 1965 = *Gymnothorax prasinus* (Richardson, 1848); and *Muraena mierszowskii* Steindachner, 1896, *Gymnothorax leucostigma* Jordan & Richardson, 1909, *Gymnothorax nirosus* Tanaka, 1918, *Muraena shirleyi* Griffin, 1933, and *Lycodontis wooliensis* Whitley, 1968 = *Gymnothorax prionodon* Ogilby, 1895. Australian morays considered to be *nomen dubia* are: *Anarchias insuetus* Whitley, 1932b; *Gymnothorax dakini* Whitley & Colefax, 1938; *Gymnothorax garsiae* Whitley & Colefax, 1938; and *Gymnothorax scriptus* Schneider, 1801. Miscellaneous notes on the changes made to the listing of Australian morays by Paxton *et al.* (1989), a discussion of the distributions of Australian and New Zealand morays, and an index to all names are provided.

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The moray eels of Australia have not received comprehensive treatment since Weber & de Beaufort's (1916) review and Munro's (1957) leaflet in the Handbook of Australian Fishes. In their zoological catalogue of Australian fishes, Paxton *et al.* (1989: 126) introduced the family Muraenidae by stating "There is no comprehensive treatment of the moray eels and the group is badly in need of revision." The fishes inhabiting the shallow tropical waters of northern Australia, including the morays, have been well sampled and are fairly well known inasmuch as many of them are part of the vast tropical fauna of the Indo-Pacific. The ichthyofauna of the cooler waters of sub-tropical and temperate southern Australia and New Zealand is less sampled and less understood. The uncertainty regarding the validity of species described from this area, and the lack of information other than the original descriptions in many cases, indicated study of the type specimens and specimens collected in this area was badly needed. Studies were pursued some years ago by the late Peter H.J. Castle and subsequently by the junior author; recently, we located and re-examined all extant type specimens in the Australian Museum, Sydney, in order to compare them with other muraenid type specimens, most of which have recently been re-examined by the authors. As a result, valid species of Australian and New Zealand waters have been determined, and an updated listing and key to species of the area is now possible.

The family Muraenidae as currently recognised is large and diverse and divided into two subfamilies, externally recognised by the extent of the fins: the Uropterygiinae with dorsal and anal fins restricted to the tail tip, and the Muraeninae with a long dorsal fin beginning near to well before the anus and with anal fin beginning just behind the anus. Fourteen genera are currently recognised: four in the Uropterygiinae (*Anarchias*, *Channomuraena*, *Scuticaria*, and *Uropterygius*), and ten in the Muraeninae (*Echidna*, *Enchelycore*, *Enchelynassa*, *Gymnomuraena*, *Gymnothorax*, *Monopenchelys*, *Muraena*, *Pseudechidna*, *Rhinomuraena*, and *Strophidon*). Of these, all but *Gymnothorax* are characterised by specific, observable external characters, such as the position of the dorsal-fin origin, the length of the tail, the nostril condition, and differences in dentition. However, a great majority of species have been lumped together in *Gymnothorax* sensu lato (with 14 generic synonyms), because characters used for separation of genera have been found to be invalid or overlapping. Thus, the generic classification used here is based on historical convention and current usage, with many species with widely varying characters all placed in *Gymnothorax*. That complex genus, as well as the species of *Anarchias* (we consider our identification of Australian species to be provisional), are in need of revision.

Muraenid species are common and widely distributed, found mainly in tropical waters, with a limited number taken in subtropical or temperate waters. Their abundance and ecological significance is always under-appreciated because of their cryptic behaviour; for example, Brock *et al.* (1979) used ichthyocides to demonstrate that morays comprised as much as 47% of the carnivorous fish biomass of a patch reef in Kaneohe Bay, Oahu. A general discussion of the family Muraenidae was published by Böhlke *et al.* (1989) in their treatment of western Atlantic morays, which

included classification, osteology, habitat, behaviour, reproduction, and taxonomic and species characters. More recently, Böhlke *et al.* (in press) treated the morays of the western central Pacific, and Böhlke & Randall (2000) reviewed the morays of Hawaii, both publications providing colour and/or black-and-white photographs of many species that are also found in Australian waters. Several recent books dealing with Australian species of fishes are available which, although not comprehensive in treatment, provide accurate identifications and useful colour photographs and paintings of many Australian muraenids. Included are: Randall *et al.* (1997) on fishes of the Great Barrier Reef; Allen (1992) on fishes of tropical Australia and southeast Asia; Kuitert (1993) on southeastern Australian coastal fishes; Gomon *et al.* (1994) on fishes of Australia's south coast; and Kuitert's (1997) guide to sea fishes of Australia, directed primarily to divers and fishermen.

A list of the 59 valid species now known to exist in Australian and New Zealand waters, with their common names, is presented in Table 1. A comprehensive key to species, including notes on coloration, vertebral counts, maximum size, and distribution for each species, is presented below. (We have not attempted to diagnose and treat most of the species that appear in the key, rather we have provided for each species a recent and competent literature source or sources that illustrate and describe those species.)

The type specimens of Australian morays in the Australian Museum, Sydney, and other museums were re-examined and additional data taken, including vertebral counts from radiographs. The information obtained has allowed confirmation of the validity of several species and confirmation of the synonymy of others. We lacked an opportunity to locate or examine types of the five species (only one of which is believed to be extant) expected to be in New Zealand museums; however, because the species are closely allied to those in Australian waters, brief summaries of the status of these names are also presented, based on original descriptions and recent information obtained from the late P.H.J. Castle (1999, in litt.). Of the 30 nominal species described from Australia and New Zealand (including the two new species), 11 are here considered valid; 15 have been put in the synonymy of previously described species; and four remain as *nomen dubium*.

We provide redescrptions of 10 valid species (along with descriptions of their type specimens and their synonyms) found in sub-tropical and temperate waters of the area, which until now have remained relatively unknown or inadequately described, plus descriptions of the two new species. They are: *Gymnothorax annasona* Whitley, 1937; *G. atolli* (Pietschmann, 1935); *G. austrinus* n.sp., *G. cephalospilus* n.sp., *G. cribroris* Whitley, 1932a; *G. longinquus* (Whitley, 1948); *G. nubilus* (Richardson, 1848); *G. obesus* (Whitley, 1932a); *G. porphyreus* (Guichenot, 1848); *G. prasinus* (Richardson, 1848); *G. prionodon*, Ogilby, 1895; and *G. woodwardi* McCulloch, 1912. That section is followed by a complete listing and comments upon the remaining Australian and New Zealand muraenid type specimens.

Several species recently listed by Paxton *et al.* (1989) in the *Zoological Catalogue of Australia* are not herein included as part of the Australian-New Zealand fauna; they

Table 1. Valid species of morays of Australia and New Zealand.

<i>Anarchias allardicei</i> Jordan & Starks, 1906	Allardice's moray
<i>Anarchias cantonensis</i> (Schultz, 1943)	Canton Island moray
<i>Anarchias leucurus</i> (Snyder, 1904)	Fine-spotted moray
<i>Anarchias seychellensis</i> Smith, 1962	Seychelles moray
<i>Echidna nebulosa</i> (Ahl, 1789)	Snowflake moray
<i>Echidna polyzona</i> (Richardson, 1845)	Barred moray
<i>Echidna unicolor</i> Schultz, 1953	Unicolor moray
<i>Enchelycore bayeri</i> (Schultz, 1953)	Bowmouth moray
<i>Enchelycore ramosa</i> (Griffin, 1926)	Mosaic moray
<i>Enchelynassa canina</i> (Quoy & Gaimard, 1824)	Indo-Pacific Viper moray
<i>Gymnomuraena zebra</i> (Shaw, 1797)	Zebra moray
<i>Gymnothorax annasona</i> Whitley, 1937	Lord Howe Island moray
<i>Gymnothorax atoll</i> Pietschmann, 1935	Atoll moray
<i>Gymnothorax austrinus</i> n.sp.	Southern moray
<i>Gymnothorax buroensis</i> (Bleeker, 1857)	Latticetail moray
<i>Gymnothorax castlei</i> Böhlke & Randall, 1999	Castle's moray
<i>Gymnothorax cephalospilus</i> n.sp.	Head-spot moray
<i>Gymnothorax chilospius</i> Bleeker, 1865	Lipspot moray
<i>Gymnothorax cribroris</i> Whitley, 1932	Sieved moray
<i>Gymnothorax enigmaticus</i> McCosker & Randall, 1982	Enigmatic moray
<i>Gymnothorax eurostus</i> (Abbott, 1861)	Indo-Pacific stout moray
<i>Gymnothorax favagineus</i> Bloch & Schneider, 1801	Honeycomb moray
<i>Gymnothorax fimbriatus</i> (Bennett, 1832)	Darkspotted moray
<i>Gymnothorax flavimarginatus</i> (Rüppell, 1830)	Yellowmargin moray
<i>Gymnothorax fuscomaculatus</i> (Schultz, 1953)	Brownspotted moray
<i>Gymnothorax gracilicaudus</i> Jenkins, 1903	Slendertail moray
<i>Gymnothorax intesi</i> (Fourmanoir & Rivaton, 1979)	Whitemargin moray
<i>Gymnothorax javanicus</i> (Bleeker, 1859)	Giant moray
<i>Gymnothorax kidako</i> (Temminck & Schlegel, 1846)	Kidako moray
<i>Gymnothorax longinquus</i> (Whitley, 1948)	Long moray
<i>Gymnothorax margaritophorus</i> Bleeker, 1865	Blackpearl moray
<i>Gymnothorax mccoskeri</i> Smith & Böhlke, 1997	McCosker's moray
<i>Gymnothorax melatremus</i> Schultz, 1953	Dwarf moray
<i>Gymnothorax meleagris</i> (Shaw, 1795)	Whitemouth moray
<i>Gymnothorax minor</i> (Temminck & Schlegel, 1848)	Lesser moray
<i>Gymnothorax monochrous</i> Bleeker, 1856	Monotone moray
<i>Gymnothorax nubilus</i> (Richardson, 1848)	Cloudy moray
<i>Gymnothorax nudivomer</i> (Günther, 1867)	Yellowmouth moray
<i>Gymnothorax obesus</i> (Whitley, 1932a)	Obese moray
<i>Gymnothorax pictus</i> (Ahl, 1789)	Peppered moray
<i>Gymnothorax pindae</i> Smith, 1962	Pinda moray
<i>Gymnothorax polyuranodon</i> (Bleeker, 1853)	Manytoothed moray
<i>Gymnothorax porphyreus</i> (Guichenot, 1848)	Lowfin moray
<i>Gymnothorax prasinus</i> (Richardson, 1848)	Yellow moray
<i>Gymnothorax prionodon</i> Ogilby, 1895	Indo-Pacific spotted moray
<i>Gymnothorax pseudoherreii</i> Böhlke, 2000	False brown moray
<i>Gymnothorax pseudothyrsoides</i> (Bleeker, 1852b)	False spotted moray
<i>Gymnothorax rueppelliae</i> (McClelland, 1844)	Banded moray
<i>Gymnothorax thyrsoides</i> (Richardson, 1845)	White-eyed moray
<i>Gymnothorax undulatus</i> (Lacepède, 1803)	Undulated moray
<i>Gymnothorax woodwardi</i> McCulloch, 1912	Woodward's moray
<i>Gymnothorax zonipectis</i> Seale, 1906	Bar-tail moray
<i>Rhinomuraena quaesita</i> Garman, 1888	Ribbon moray
<i>Strophidon sathete</i> (Hamilton, 1822)	Longtail moray
<i>Uropterygius concolor</i> Rüppell, 1838	Unicolor snake moray
<i>Uropterygius fuscoguttatus</i> Schultz, 1943	Brownspotted snake moray
<i>Uropterygius marmoratus</i> (Lacepède, 1803)	Marbled snake moray
<i>Uropterygius micropterus</i> (Bleeker, 1852)	Shortfinned snake moray
<i>Uropterygius nagoensis</i> Hatooka, 1984	Nago snake moray

include names that have been found to be junior synonyms of other species, names considered to be *nomen dubia*, and/or species incorrectly identified (see under “Miscellaneous remarks” below). We herein add 13 species to their list: *Gymnothorax annasona*, now considered to be a valid species; *G. atolli*, a previously unrecognised species from Australia; *G. minor* (specimens previously identified as *G. scriptus* are this species); *G. porphyreus*, numerous specimens identified from the area; *G. enigmaticus*, previously unreported from NE Australia; three recently described species (*G. castlei* Böhlke & Randall, 1999; *G. mccoskeri* Smith & Böhlke, 1997; and *G. pseudoherrei* Böhlke, 2000); *Anarchias cantonensis* and *A. leucurus*, reported by Randall *et al.* (1997) from “Great Barrier Reef Waters”; and the two new species.

Methods

Methods and terminology are as defined in Böhlke (1989). Proportions are expressed in terms of total length (TL), measured from the snout tip to the tip of the tail, or head length (HL), from snout tip to the posterodorsal margin of the gill opening. Preanal length is measured from snout tip to mid-anus; body depth is measured at the gill opening and at the anus and does not include the fins; snout length is measured from snout tip to the anterior margin of the eye; upper-jaw length is from snout tip to the external inner angle of the mouth, lower-jaw length from tip of lower jaw to the external inner angle of the mouth. Head pores are few, with little variation (noted in species accounts only when atypical); morays typically have 3 supraorbital pores (1 ethmoid + 2 on dorsal snout), 4 infraorbital pores, 6 mandibular pores, and 2 branchial pores. Tooth counts are approximate and include sockets of missing teeth. Vertebral counts are obtained from radiographs as explained in Böhlke (1982); the mean vertebral formula (MVF) is expressed as the mean value for predorsal-preanal-total counts for each species. Institutional abbreviations follow Leviton *et al.* (1985).

Notes on distribution. We have defined the distribution of all species in the key and text using geographical locations that in some cases coincide with the boundaries of Australian states. The regions that we recognise are not biologically unique but may be useful in a general analysis of reef fish distribution. We define the regions as follows: **northeast (NE)**, from Cape York (15°S 143°E) to the southeastern border of Queensland; **southeast (SE)**, from northern New South Wales to eastern Victoria; **south (S)**, from the

southeastern border of South Australia to Cape Leeuwin (115°S 34°E), the southwest corner of Western Australia; **west (W)**, from Cape Leeuwin north to the Northwest Cape (22°S 114°E) of Western Australia; **northwest (NW)**, from the Northwest Cape to the western boundary of Northern Territories; **north (N)**, from the western boundary of Northern Territories to Cape York, Queensland, including the Gulf of Carpentaria.

Cautionary note concerning key: Morays are extremely difficult to identify because many characters show great variability. Proportions, dentition, and coloration may vary due to growth, sexual condition, means and length of preservation, and other factors, thus making the construction and use of a key difficult. The following key should allow identification of “typical” adult specimens, based on dentition and, from couplet 20 on, largely on coloration. Juveniles often exhibit colour patterns that differ considerably from those of the adults. The colour may be distinct and contrasting, changing to become diffuse, dark and/or obscure in large specimens; juveniles often have more and additional rows of teeth, adults may have fewer teeth or lack some entirely, or conversely may have additional rows of teeth. Coloration is not only variable, but also difficult to describe; while some species exhibit distinctive coloration, some do not; what may appear to one person (or in one specimen) as diffuse pale blotches on a dark body may appear to another (or in another specimen) as dark reticulations on a pale body; both possibilities should be pursued when using the key, particularly where additional characters given may aid in identification.

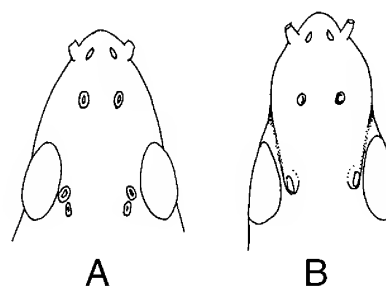


Figure 1. A, posterior nostril contiguous with supraorbital pore in all species of *Anarchias*. B, posterior nostril not contiguous with supraorbital pore, the condition of all species of *Uropterygius*.

Key to the species of Moray Eels of Australia and New Zealand

Abbreviations: TL, total length; V, total vertebrae; MVF, mean vertebral formula. Vertebral numbers may include those from specimens extralimital to Australia and New Zealand. References that provide illustrations and diagnostic characters are indicated in the key by superscript numbers as follows: 1—this study; 2—Allen, 1985; 3—Böhlke, 1997; 4—Böhlke, 2000; 5—Böhlke & Randall, 1999; 6—Böhlke & Randall, 2000; 7—Castle & McCosker, 1986; 8—Kuitert, 1993; 9—McCosker *et al.*, 1984; 10—Myers, 1999; 11—Randall *et al.*, 1997; 12—Randall & Golani, 1995; and 13—Smith & Böhlke, 1997.

- 1 Dorsal and anal fins restricted to tail tip; teeth needle-like and pointed subfamily Uropterygiinae 2
- Dorsal-fin origin near or before anus; anal-fin origin just behind anus; teeth molariform, rounded, pointed, or caniniform subfamily Muraeninae 10
- 2 Posterior nostril contiguous with an enlarged supraorbital pore, appearing as a double pore (Fig. 1A); adults small, not exceeding 30 cm *Anarchias* 3
- Posterior nostril not contiguous with a supraorbital pore (Fig. 1B) most adults small to medium-length, few species exceed 50 cm *Uropterygius* 6
- 3 Supraorbital pore slightly in advance of centre of eye; body coloration nearly uniform brown, or brown with a network of wide brownish lines, more or less arranged into irregular vertical reticulated bars 4
- Supraorbital pore either in line with or slightly behind centre of eye; body coloration either with pale reticulations or pale, stellate blotches 5
- 4 Body nearly uniform brown, dorsal fin darker, the tail tip white; head sometimes with a pale bar behind eye, the head pores white; V 97-102; MVF 88-89-99; to 17 cm; W, NW, NE Australia, West Pacific *Anarchias allardicei* Jordan & Starks, 1906¹⁰
- Body pale, overlain with a network of wide brownish lines arranged into irregular vertical reticulated bars, more obvious posteriorly; underside of head usually pale, the head pores white; V 101-108; MVF 91-93-104; to 20 cm; NE Australia, Indo-Pacific *Anarchias cantonensis* (Schultz, 1943)¹⁰
- 5 Body varies from nearly uniform brown, through brown mottled with pale brown, to brown with three or four rows of stellate pale blotches; throat pale, the lower jaw often mottled with brown; V 121-132; MVF 111-117-126; to 29 cm; W, NW, SE Australia, widespread in Indo-Pacific from Easter Island to Africa *Anarchias seychellensis* Smith, 1962⁵
- Body brown overlain with a faint whitish reticulation on the upper body; chin and throat pale; V 106-112; MVF 98-100-110; to 25 cm; NE Australia, Indo-Pacific to Hawaii *Anarchias leucurus* (Snyder, 1904)⁵
- 6 Body in life and in preservative uniform tan to gray; jaw teeth biserial; V 117-124; MVF 110-114-120; to 32 cm; W, NW Australia, Indo-Pacific *Uropterygius concolor* Rüppell, 1838^{7,9}
- Body in life and in preservative mottled, spotted, or reticulated; jaw teeth biserial or triserial 7

- 7 Jaw teeth biserial; body pale to gray, overlain above midline with a reticulated network of fine brown lines; V 113-119; MVF 106-108-117; a small species, to 30 cm; NE Australia, Indo-Pacific *Uropterygius micropterus* (Bleeker, 1852a)^{8,9}
- Jaw teeth triserial; body coloration not as above; may attain a larger size, to 60 cm 8
- 8 Coloration of anterior half of body and posterior trunk region notably different; head and chin plain, body uniform brown anteriorly, tail covered by numerous dark brown spots (about equal to eye); V 113-124; MVF 99-104-119; to 30 cm; NE Australia; Indo-Pacific to Hawaii *Uropterygius fuscoguttatus* Schultz, 1953^{5,10}
- Coloration of head, trunk and body similar, with either reticulations or indistinct spotting; V 131-144 9
- 9 Mouth large, snout short; body yellow anteriorly, brown posteriorly, overlain with reticulated broad, dark brown lines; V 139-144; MVF 118-124-140; to 71 cm; NE Australia, western Pacific *Uropterygius nagoensis* Hatooka, 1984^{9,12}
- Mouth and snout moderate in size; body cream to gray, overlain with numerous dark roundish spots; V 131-139; MVF 124-126-135; to 62 cm; NE Australia; Indo-Pacific *Uropterygius marmoratus* (Lacepède, 1803)^{5,9}
- 10 Snout and jaws short, lower jaw shorter; teeth low and rounded or molariform, no caniniform teeth; teeth in upper jaw usually biserial; vomerine teeth molariform and continuous with median intermaxillary teeth 11
- Snout short to elongate, jaws usually about equal; some teeth sharp or caniniform; teeth in upper jaw uniserial or biserial; vomerine teeth molariform, rounded, or sharp, separated from median intermaxillary teeth 14
- 11 Anus posterior to midbody, tail about 30% of TL; body coloration dark brown to black, encircled by many narrow white to yellow rings; V 129-137; MVF 14-84-132; to 150 cm; W, NW, NE Australia, widespread in Indo-Pacific from Africa to eastern Pacific *Gymnomuraena zebra* (Shaw, 1797)^{5,11}
- Anus about at mid-body, tail about 50% of TL *Echidna* 12
- 12 Body coloration uniform; V 117-127; MVF 6-52-122; to 36 cm; W, NW Australia, Indo-Pacific *Echidna unicolor* Schultz, 1953^{2,10}
- Body coloration blotched or barred 13
- 13 Body pale with 2 rows of stellate black blotches with pale (yellow or orange in life) centres; V 121-126; MVF 6-57-122; to 75 cm; W, NW, N, NE, SE Australia, Indo-Pacific from Africa to eastern Pacific *Echidna nebulosa* (Ahl, 1789)⁵
- Body with 20–30 contrasting dark and pale bars or rings encircling the body in young, becoming mottled brown and indistinct with age but bars visible near end of tail; V 119-126; MVF 6-52-122; to 72 cm; NE Australia, Indo-Pacific *Echidna polyzona* (Richardson, 1845)⁵

- 14 Body slender and very elongate, its depth 40× or more in TL..... 15
- Body stouter, its depth 30× or less in TL 16
- 15 Anterior nostrils simple tubes; chin lacks barbels; body cylindrical; body uniform brown, fins darker; V 185-208; MVF 9-78-197; to 394 cm; N, NW, NE Australia, Indo-Pacific *Strophidon sathete* (Hamilton, 1822)^{3, 11}
- Anterior nostrils with broad foliose enlargements; lower jaw tip with protruding barbels; body and tail laterally compressed; body yellow, black, or bright blue, fins yellow or white; V 276-281; MVF 5-90-278; to 130 cm; W, NE Australia, Indo-Pacific *Rhinomuraena quaesita* Garman, 1888¹¹
- 16 Jaws elongate and arched, meeting only at their tips; elongate canine teeth exposed when jaw is closed 17
- Jaws not elongate and arched, closing completely or for most of their length; teeth not exposed when jaw is closed *Gymnothorax*.... 19
- 17 Anterior nostrils with bilobate flaps on posterior margins; posterior nostrils in short, broad tubes; body uniform dark brown, fin margin paler; V 141-147; MVF 6-63-142; to 152 cm; NE Australia, Indo-Pacific to tropical eastern Pacific *Enchelynassa canina* (Quoy & Gaimard, 1824)⁵
- Anterior nostrils without large flaps; body coloration various, either uniform dark brown or patterned *Enchelycore*.... 18
- 18 Body uniform brown with narrow pale (yellow in life) margin on fins; V 146-153; MVF 10-51-149; to 70 cm; N, NW, NE Australia, Indo-Pacific *Enchelycore bayeri* (Schultz, 1953)¹¹
- Body pale, overlain with striking brown to dark mosaic pattern over entire body and fins; V 145-151; MVF 6-56-150; to 150 cm; SE Australia, New Zealand; Easter Island *Enchelycore ramosa* (Griffin, 1926)⁸
- 19 Head small, jaws short; maxillary teeth in 2 short rows ending below posterior eye; no long caniniform teeth 20
- Head large, jaws moderate to long; maxillary teeth in 1–2 rows extending to corner of mouth; caniniform teeth present 23
- 20 Dorsal-fin origin closer to anus than to gill opening; body light brown with diffuse brown mottling forming spots posteriorly; head pores in conspicuous white spots; fins pale; V 110-118; MVF 37-48-117; to 20 cm; W, NW, NE Australia, Indo-Pacific *Gymnothorax fuscomaculatus* (Schultz, 1953)⁵
- Dorsal-fin origin before gill opening..... 21
- 21 Gill opening in conspicuous dark spot; body tan to brown, sometimes with faint dark reticulations; V 132-149, MVF 4-53- 139; to 30 cm; W, NW, NE Australia, tropical Indo-Pacific *Gymnothorax melatremus* Schultz, 1953⁵
- Gill opening not in dark spot; colour not as above 22
- 22 Body and head uniformly pale; lines of small black dots marking head papillae; V 115-124; MVF 5-48-120; to 25 cm; NE Australia, Indonesia and Philippines *Gymnothorax castlei* Böhlke & Randall, 1999⁵
- Body and fins with overlapping small brown spots; tip of snout and lower jaw pale, eye white in life; V 125-137; MVF 4-50-133; to 65 cm; NW, N, NE, SE Australia to 34°S, Indo-Pacific..... *Gymnothorax thyrsoideus* (Richardson, 1845)^{8, 11}

- 23 Body pale overlain with wide, dark bars, saddles, or spots forming bars 24
- Body uniformly colored or marked other than described above 27
- 24 Body overlain with dark bars that meet along ventral surface; head barred but without spots; teeth smooth, long fangs present 25
- Body overlain with either bars or with dorsal saddles; head spotted; jaw teeth with fine serrations (may be difficult to discern), no fang-like teeth 26
- 25 Anterior nostril black; chin and throat bands reach just below lateral midline, not joined ventrally; a black spot at corner of jaw; V 125-135; MVF 5-52-131; to 75 cm; NE Australia, tropical Indo-Pacific *Gymnothorax rueppelliae* (McClelland, 1844)⁵
- Anterior nostril pale; chin and throat bands continuous; jaw corner pale; V 126-134; MVF 4-51-130; to 58 cm; NE Australia, tropical Indo-Pacific *Gymnothorax enigmaticus* McCosker & Randall, 1982¹⁰
- 26 22–30 dorsal pairs of large saddle-like brown spots each associated with smaller ventral spot, forming diffuse broad bars; V 125-130; MVF 6-51-127; to 36 cm; W and NE Australia *Gymnothorax mccoskeri* Smith & Böhlke, 1997¹³
- 15–22 spotted dark bars well defined ventrally and continuous around anal fin, but obscured above lateral line; V 129-143; MVF 6-55-139; to 55 cm; southern population from W and NE Australia (V 129-135), northern population from Japan to S China (V 135-143) *Gymnothorax minor* (Temminck & Schlegel, 1846)¹³
- 27 Body coloration uniform (brown, yellow, or green in life), lacking spots, bars, or complex pattern 28
- Body patterned with pale or dark spots, blotches, or complex reticulations 33
- 28 Snout and jaws elongate; long fang-like teeth present 29
- Snout and jaws relatively short; teeth moderate, sharp, but none fang-like 30
- 29 Coloration uniform tan to brown (may be paler ventrally), without contrasting marks; V 136-143; MVF 4-58-139; to 75 cm; W, NW Australia, tropical Indo-Pacific *Gymnothorax monochrous* Bleeker, 1856⁷
- Coloration uniform medium to dark brown (appearing green or yellow in life); pale streak on head dorsally, head pores dark; V 134-140; MVF 5-58-137; to 80 cm; W, S, SE Australia, Tasmania, New Zealand, all south of 26°S *Gymnothorax prasinus* (Richardson, 1848)^{1, 8}
- 30 Coloration uniform medium brown; no contrasting marks on head or fins; jaw teeth smooth; V 110-118; MVF 6-47-114; a small species, to 30 cm; NE Australia, western Pacific and Indian Ocean *Gymnothorax pseudoherrei* Böhlke, 2000⁴
- Coloration uniform brown, with contrasting marks on head and/or fins; jaw teeth serrate 31

- 31 Body and fins uniform brown; posterior jaw pores in pale spots;
V 127-133; MVF 5-53-131; a small species, to 30 cm; Lord Howe
Island; Hawaii and Red Sea *Gymnothorax atoll* (Pietschmann, 1935)^{1,5}
—— Body coloration uniform brown; fins with contrasting colour 32
- 32 Body and fins uniform medium brown; narrow pale margin on
fins; snout, dorsal head, and jaw pores dark; VF 6-68-151; to 88
cm; SE Australia *Gymnothorax austrinus* n.sp.¹
—— Body dark brown shading to darker brown to black on posterior
fins and tail; V 110-124; MVF 6-44-121; to 39 cm; NE Australia,
Indo-Pacific *Gymnothorax pindae* Smith, 1962⁵
- 33 Body relatively stout, depth at anus equal to or greater than depth
at gill opening, tail rounded; teeth numerous, no long fangs;
intermaxillary teeth in 5 rows across, maxillary teeth biserial for
all of their length 34
—— Body elongate, depth at anus less than depth at gill opening, tail
tapering; teeth fewer, long fangs usually present; intermaxillary
teeth usually in 3 rows across, maxillary teeth uniserial or biserial
anteriorly 36
- 34 Head and body dark brown or black with numerous distinct small
pale spots that extend onto snout; tip of tail pale (yellow in life),
inside of mouth pale (white in life); V 127-132; MVF 5-52-130; to
100 cm; NE Australia, Indo-Pacific to Galápagos Islands *Gymnothorax meleagris* (Shaw, 1795)⁵
—— Body dark with darker spots or with both pale and dark spots;
inside of mouth not pale, tail tip patterned 35
- 35 Body dark with darker spots and mottling, some spots appearing
in rows along body; anterior head region uniformly dark or
indistinctly mottled; V 109-117; MVF 5-47-113; to 39 cm; W,
NW, NE Australia, tropical Indo-Pacific to tropical eastern
Pacific *Gymnothorax buroensis* (Bleeker, 1857)⁵
—— Body colour highly variable, tan to brown with small pale spots
(yellow in life) with dark spots superimposed, sometimes
appearing as reticulated pattern on tail; head spotted; V 116-125;
MVF 5-48-120; to 58 cm; W, NW, NE and SE Australia, Indo-Pacific,
an antitropical species found poleward of 15°S *Gymnothorax eurostus* (Abbott, 1861)⁵
- 36 Body spotted, with discrete spots or with indistinct spots or
blotches 37
—— Body with complex pattern of reticulations often forming vertical
bars posteriorly 54
- 37 Pale spots or blotches on dark background or pale spots separated
by dark reticulum 38
—— Dark spots on pale background or dark spots separated by pale
reticulations 45
- 38 Pale spots distinct, about equal to or less than eye 39
—— Pale spots diffuse, appearing as blotches, or separated by dark
reticulum, larger than eye 42

- 39 Distinct white spotting on head and anterior trunk, none or very few on tail; white margins on entire length of fins; V 142-146; MVF 6-64-145; to 20 cm; NW and NE Australia *Gymnothorax cephalospilus* n.sp.¹
- Head, body, and tail spotted, but not predominantly on head and anterior trunk 40
- 40 Head, body, tail and fins medium to dark brown covered with small, close-set, pale spots of irregular shape, the spots similar on head, body, and fins; V 166-172; MVF 10-70-169; to 170 cm; SE Australia and New Zealand *Gymnothorax obesus* (Whitley, 1932a)¹
- Head, body and tail with pale spots of varying sizes, some widely-separated or ocellated 41
- 41 Largest teeth serrate; small spots on head close-set, becoming fewer, larger and ocellate on tail; fins with pale margin; mouth bright yellow in life; V 131-139; MVF 3-52-134; to 100 cm; NE Australia, tropical Indo-Pacific *Gymnothorax nudivomer* (Günther, 1867)⁵
- Teeth smooth; small spots on head, becoming larger and segmented on body, sometimes ocellate on tail; fins with 1–2 rows spots; V 138-142; MVF 5-55-140; to 87 cm; SE Australia, New Zealand, Taiwan and Japan *Gymnothorax prionodon* Ogilby, 1895^{1, 8}
- 42 Body dark brown to blackish, with large scattered indistinct grayish blotches; fins dark with black margin; head pores with fine brown rims; V 129-137; MVF 5-60-133; to 74 cm; W, NW, NE Australia, Thailand? *Gymnothorax longinquus* (Whitley, 1948)¹
- Body tan to brown with large pale spots or blotches; fins with pale margins 43
- 43 Teeth serrate; head dusky or reticulated, body and tail with irregular pale spots separated by narrow dark reticulum; fins with pale or white margins; V 147-163; MVF 5-68-155; to 103 cm; NE Australia, central and western Pacific and Indian oceans, a deep-water species *Gymnothorax intesi* (Fourmanoir & Rivaton, 1979)
- Teeth smooth 44
- 44 Overall coloration brown with large, pale, snowflake-like blotches on head, body and fins (sometimes fewer and smaller on tail), colour of uniform intensity; anal fin with conspicuous pale margin; V 136-149; MVF 5-55-141; to 92 cm; NE Australia, Hawaii, Japan, Taiwan, Society Islands *Gymnothorax kidako* (Temminck & Schlegel, 1846)⁵
- Body tan with about 3 rows of large pale spots dorsally; head, abdomen, and ventral tail region pale and unspotted; anal fin dark basally with narrow pale margin; V 134-141; MVF 4-57-137; to 58 cm; W and S Australia *Gymnothorax woodwardi* McCulloch, 1912¹
- 45 Dark spots as large as or larger than eye 46
- Dark spots small and round, sometimes overlapping or sometimes aggregating to form complex pattern 49

- 46 Gill opening in a prominent dark blotch; juveniles tan with distinct dark spots on head, body, and fins, the spots becoming large and diffusely speckled with pale spots in adults; fins pale in juveniles, patterned in adults; V 137-143; MVF 6-60-141; to 250 cm; NW, N, NE Australia, tropical Indo-Pacific to tropical eastern Pacific *Gymnothorax javanicus* (Bleeker, 1859)⁵
- Gill opening not in a prominent dark blotch 47
- 47 Dorsal-fin origin behind gill opening (but fins obscured by flabby flesh, often mistaken as a species of *Uropterygius*); coloration tan with large irregular dark spots on head, body, and fins; a series of elongate spots forming 5–7 horizontal lines in branchial area; snout and lower jaw pale; V 141-148; MVF 12-70-144; to 70 cm; NE Australia, western Pacific, inhabits estuaries or rivers *Gymnothorax polyuranodon* (Bleeker, 1853)
- Dorsal-fin origin before gill opening; dark spots polygonal on body, interspaces appearing as a reticulum 48
- 48 Color pattern uniform on head, body and fins; large, black, polygonal spots separated by a narrow, pale reticulum (in small specimens the spots are rounder and the reticulum is wider); V 138-144; MVF 5-60-141; to 110 cm; NW, N, NE, SE Australia, tropical Indo-Pacific *Gymnothorax favagineus* Bloch & Schneider, 1801¹²
- Head uniform brown or mottled; body and fins with irregular brown rectangular spots separated by a narrow pale reticulum; V 126-138; MVF 5-53-132; to 150 cm; NW, N, NE Australia, tropical Indo-Pacific to eastern Pacific *Gymnothorax undulatus* (Lacepède, 1803)⁵
- 49 Dark spots small and round, may be overlapping but not aggregating to form a complex pattern 50
- Dark spots aggregating to form a complex pattern of larger spots 52
- 50 Dark spots few, eye-sized and well-separated; body tan with 2–4 rows of spots along trunk and tail, abdomen unspotted; a conspicuous series of about 5 spots in 2 oblique rows behind eye; V 128-142; MVF 5-54-133; to 68 cm; W, NW, NE Australia, Indo-Pacific *Gymnothorax fimbriatus* (Bennett, 1832)¹¹
- Dark spots numerous, small and close-set or overlapping 51
- 51 Gill opening in a dark blotch; head, body and fins with overlapping dark spots; posterior fins with narrow pale margins (yellow or green in life); V 132-140; MVF 5-58-136; to 120 cm; NW, N, NE Australia, Indo Pacific, occasionally to eastern Pacific *Gymnothorax flavimarginatus* (Rüppell, 1830)⁵
- Gill opening not dark; body dark with darker mottling and spots on head, body, and fins; snout, nostrils and head pores dark; V 137-144; MVF 6-58-141; to 130 cm; Kermadec, Lord Howe, and Norfolk islands, New Zealand; Easter Island, Chile and Peru *Gymnothorax porphyreus* (Guichenot, 1848)¹
- 52 Dorsal-fin origin above or near gill opening; vomerine teeth biserial, diverging anteriorly in adults; colour highly variable: juveniles pale with irregular dark spots, unspotted ventrally; spots usually spreading onto abdomen with growth; adults pale with small dark dots that aggregate to form large dark rosettes in 2–3 rows along body; some large adults very dark overall, with rows

- of darker rosettes; V 128-135; MVF 9-58-131; to 140 cm; NW, N, NE Australia, tropical Indo-Pacific to eastern Pacific *Gymnothorax pictus* (Ahl, 1789)⁵
- Dorsal-fin origin well before gill opening 53
- 53 Body pale with small dark spots aggregating to form larger spots forming about 4 irregular rows along body; pattern present on top of head; fins patterned, with narrow pale margin posteriorly; V 122-135; MVF 4-56-130; to 80 cm; NW Australia, western Pacific *Gymnothorax pseudothyrsoides* (Bleeker, 1852b)¹¹
- Body gray or brown with dark spots on head, body, and fins, with aggregations of larger dark spots forming scattered larger blotches; fins patterned basally, anal fin with conspicuous pale margin; V 141-144; MVF 5-58-142; to 55 cm; Middleton and Elizabeth Reefs and Lord Howe Island *Gymnothorax annasona* Whitley, 1937¹
- 54 Dark spots on head 55
- Both dark and pale marks on head 57
- 55 Lines of faint, small dark dots marking head papillae and anterior lateral-line papillae; body with brown and pale reticulations forming cloud-like spots; V 130-134; MVF 4-52-132; to 68 cm; Norfolk and Kermadec islands, New Zealand *Gymnothorax nubilus* (Richardson, 1848)¹
- Conspicuous dark spots behind eye 56
- 56 Single row of 3–5 dark oval blotches in a line behind eye extending onto anterior trunk region; body with brown and pale vertical reticulations; V 123-133; MVF 6-50-129; to 47 cm; NW, NE Australia, Indo-Pacific *Gymnothorax margaritophorus* (Bleeker, 1865)¹¹
- 2–3 rows of prominent dark brown spots (equal to or smaller than eye) behind eye; body with pale and brown lattice-like reticulations, sometimes appearing as pale spots on tail; V 116-125; MVF 4-50-120; to 46 cm; NW, NE, SE Australia, to 34°S *Gymnothorax cribroris* Whitley, 1932a^{1, 8}
- 57 Jaw pores not in white spots; head brown, marked dorsally from snout to occiput with a pale dorsal streak with brown borders; body tan, overlain with dark brown, irregular oblique bars extending from dorsum to midflank anteriorly, extending ventrally and onto dorsal fin on tail; V 127-135; MVF 5-51-131; to 32 cm; NE Australia, Indo-Pacific *Gymnothorax gracilicaudus* Jenkins, 1903⁵
- Jaw pores in white spots 58
- 58 Posterior 2–3 pores of upper and lower jaws in pale spots, extending as a distinct pale blotch from upper to lower jaw; a distinct brown spot at corner of mouth; body and tail with complex, lichen-like blotches; V 120-129; MVF 5-49-125; to 50 cm; NW, NE Australia, tropical Indo-Pacific *Gymnothorax chilospilus* Bleeker, 1865⁵
- Posterior 2–3 pores of upper and lower jaws enclosed by white bars that are continuous across lower jaw; a distinct irregular brown mark with pale borders behind eye; body with pattern of oblique broken vertical bars that become dark with bright white borders on posterior fins; V 123-130; MVF 6-48-126; to 47 cm; W, NW, NE Australia, tropical Indo-Pacific *Gymnothorax zonipectis* Seale, 1906¹¹

**Rare and poorly known species
of Australian *Gymnothorax***

***Gymnothorax annasona* Whitley, 1937**

Lord Howe Island moray

Fig. 2

Gymnothorax flavimarginatus annasona Whitley, 1937: 220. Holotype AMS IA.6867, 19 inches (current measurement 508 mm) TL; Middleton Reef, N of Lord Howe Island, near the “Annasona” wreck, spear; Mr Tom Patton; 18 April 1936.

Description. A moderately large, elongate moray, depth at gill opening 13–21, depth at anus 15–25 in TL; anus before midbody, preanal length 2.1–2.4. Head moderately elongate, 7.2–8.4 in TL; snout moderately long and tapering, 4.7–5.5 in HL; jaws long, upper jaw 2.2–2.7 in HL. Eye moderate, 8.0–13 in HL, above midgape. Anterior nostril in long narrow tube; posterior nostril a pore above and behind anterior margin of eye. Head pores typical; two branchial pores above and just before gill opening; dorsal-fin origin above or before first pore, closer to gill opening than to rictus. Gill opening at midside. Predorsal vertebrae 4–6, preanal vertebrae 56–59, total vertebrae 141–144; MVF 5-58-142 (9).

Teeth large, triangular and smooth, uniserial in adults. Outer intermaxillary teeth 6 plus 1–4 (usually 3) tiny teeth between posterior teeth; 3 long median fangs. Maxillary teeth of small specimens (to 350 mm) an inner row of 1–4 long teeth and outer row of 11–18 teeth, tapering in size posteriorly; large specimens with an outer row of 11–13 teeth only. Vomerine teeth small and hidden, 6–11 in single

row. Dentary teeth of small specimens 3–5 large inner teeth enclosed by 4–8 small outer teeth, continuing as row of 11–18 teeth; large specimens with single row of 15–18 teeth, large anteriorly, tapering in size posteriorly.

Coloration mottled and spotted on head, body and fins. Head with small spots, body and tail covered with small overlapping rounded dark spots, overlain with scattered larger dark blotches formed by aggregations of darker spots. Dorsal fin high, with basal coloration like body, the margin pale for posterior third to two-thirds of fin; anal fin spotted basally, with conspicuous pale margin for entire extent.

Notes on holotype. The holotype of *Gymnothorax annasona* is hard and dry, and has a missing and regenerated tail (as noted by Whitley); its total length (508+ mm) is longer than Whitley’s stated 19 inches (483 mm). Coloration as described above. Proportions and meristics are imprecise due to the missing tail; VF 4-58-133+. Teeth large, triangular and smooth, few in number; intermaxillary teeth in three rows with two median fangs; maxillary, vomerine, and dentary teeth uniserial.

Remarks. The largest specimen we examined is 750 mm; it is said to reach 1500 mm (Coleman, 1983: 40). None of the study specimens is mature; a 553 mm specimen is an immature female. It has been taken at Middleton and Elizabeth Reefs, and Lord Howe Island, all off New South Wales, in the Tasman Sea, 29–32°S. It is common at Lord Howe Island where it was seen in shallow waters of coral reefs at depths to 15 m, observed lurking in crevices during the day and actively swimming at night (John E. Randall, pers. comm.). Its life colors in an underwater colour photo

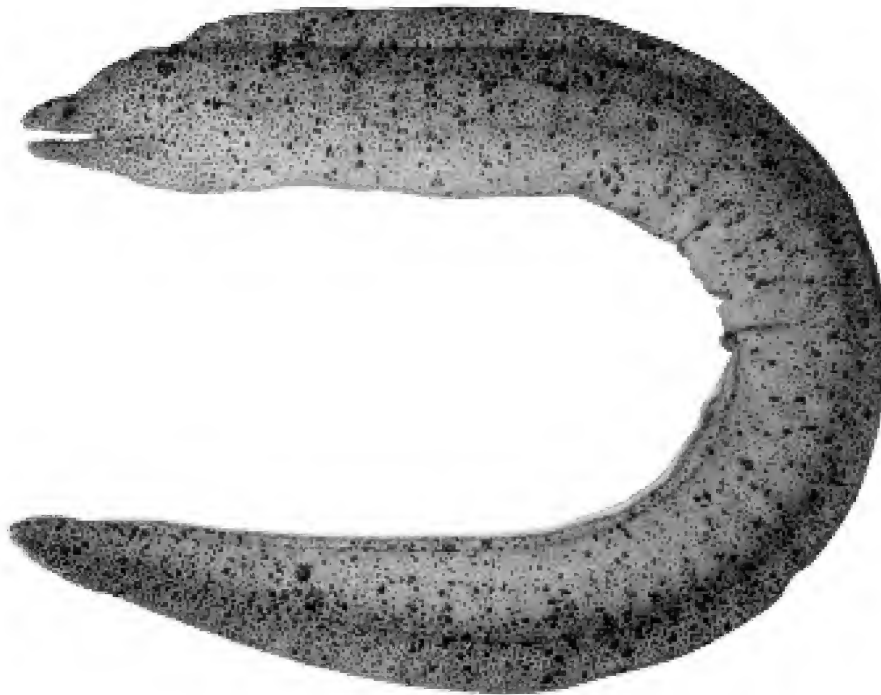


Figure 2. *Gymnothorax annasona*; 705 mm TL, Lord Howe Island, photo by J.E. Randall.

(Coleman, 1983: 40) are dark brown spots on a yellowish-tan background.

Gymnothorax annasona was described as a subspecies of *G. flavimarginatus*, a common tropical species with somewhat similar coloration but that lacks the large aggregates of spots, has a prominent black blotch surrounding the gill opening, and also has fewer vertebrae (MVF 5-58-136). We elevate Whitley's subspecies to species rank, based on the differences in coloration and vertebral counts seen in the holotype and additional specimens. It is also similar to *Gymnothorax parini* from Walters Shoals in the western Indian Ocean, which has a lichenous colour pattern, a more prominent bright margin on the fins, and more vertebrae (MVF 4-56-147).

Study material. Fourteen specimens, 163–750 mm TL. MIDDLETON REEF: AMS IA.6867, 508 mm, holotype of *Gymnothorax flavimarginatus annasona*; CAS 87882, 2: 163–232 mm. ELIZABETH REEF: AMS I.27157–100, 238 mm. LORD HOWE ISLAND: AMS I.10662, 551 mm; AMS I.12099, 750 mm; AMS I.17369–006, 3: 320–481 mm. I.20257–018, 538 mm; BPBM 14777, 553 mm; BPBM 14838, 340 mm; BPBM 14867, 2: 218–238 mm.

Gymnothorax atolli (Pietschmann, 1935)

Atoll moray

Fig. 3

Heteromyrus atolli Pietschmann, 1935: 93 (holotype NMW 65106; type locality South East Island, Pearl and Hermes Reef, Hawaiian Islands).

Gymnothorax sp. A. Allen *et al.*, 1976: 377 (Lord Howe Island). *Gymnothorax australicola*. (Not of Lavenberg, 1992). Lavenberg, 1992: 59 (1 paratype, BPBM 14945 from Lord Howe Island).

Description. A small, moderately elongate moray, depth at gill opening 17–22 and depth at anus 22–27 in TL; anus before midbody, preanal length 2.0–2.2 in TL. Head moderate, its length 7.4–9.1 in TL; snout short and rounded, overhanging lower jaw, 5.2–7.0 in HL; upper jaw short, 2.6–3.3 in HL; lips papillose. Eye small, 10–14 in HL, notably closer to rictus than to snout tip. Anterior nostril in moderate tube; posterior nostril above and behind anterior margin of eye, with raised crenulate rim. Only one branchial pore, above and before gill opening; remaining head pores typical; dorsal-fin origin about midway between rictus and gill opening, above and before branchial pore. Gill opening inconspicuous, a diagonal slit at midbody. Predorsal vertebrae 4–6, preanal vertebrae 51–55; total vertebrae 127–133; MVF 5-53-131 (8).

Teeth stout and triangular, largest intermaxillary and dentary teeth serrate; maxillary teeth biserial. Peripheral intermaxillary teeth 5–6, the posterior three large and serrate; 0–2 median teeth, the second long, thin and depressible. Inner row of 8–14 tall, slender, well-spaced maxillary teeth; outer row of 15–24 short rounded teeth. On vomer 4–12 short conical teeth in irregular row. On dentary main row of 12–18 consisting of 3–5 large triangular serrate anterior teeth followed by 9–14 progressively smaller teeth; 1–4 small outer teeth flanking the large anterior teeth.

Coloration of head, body and fins medium brown; the small Hawaiian specimens uniformly colored with few pale areas, the two largest specimens (244–293 mm) mottled all over with pale blotches. Fins of some specimens pale, those of patterned specimens with body pattern. Ventral surface of head and abdomen sometimes pale. Eye ringed with dark brown pigment; head pores large and conspicuous, the anterior pores with brown pigmented rims and the posterior 1–2 upper jaw pores and the last 2–3 mandibular pores in white areas (these not obvious in patterned specimens); branchial pore small, with a fine brown-pigmented rim. Small specimens coated with mucus.

Notes on holotype. Described as *Heteromyrus atolli*, this species was largely ignored since its description until recent re-examination of the holotype indicated that it is a valid species with characters and coloration as described above (see Böhlke & Randall, 2000: 228).

Remarks. *Gymnothorax atolli* is a small species, the largest known specimen 293 mm TL; two females (206–244 mm) had 0.8–0.9 mm eggs. It is found in the Hawaiian Islands, from Pearl and Hermes Reef in the north and from Midway Atoll, the Midway specimens collected at depths to 8 m. Three additional specimens from disjunct localities of Japan, Lord Howe Island, and the Red Sea (two of them larger and with mottled coloration), were thought to perhaps represent a new species (the Red Sea specimen is desiccated, in poor condition and missing the end of its tail). They were re-examined during the course of this study and are now considered to represent larger specimens of *G. atolli* with slightly different coloration. The paratype of *G. australicola* from Lord Howe Island (BPBM 14945), which was conspicuous in having a vertebral count much lower than that of any of the other types, is this species.

Gymnothorax atolli is characterised by its overall brown or mottled coloration, single branchial pore, some serrate teeth and biserial maxillary dentition. It most similar to *G. australicola*, which also is a small brown moray with one

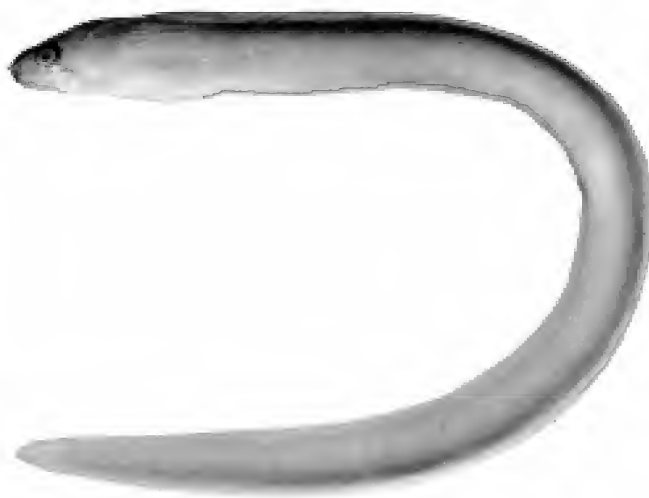


Figure 3. *Gymnothorax atolli*; BPBM 34833, 160 mm TL, Midway Atoll, photo by J.E. Randall.

branchial pore, some teeth serrate, and biserial maxillary teeth; *G. australicola* differs in having a shorter preanal length (2.2–2.5 for *australicola*, vs. 2.0–2.2 for *atolli*) and more vertebrae (MVF 5-53-144 vs. 5-53-131 respectively).

Study material. Ten specimens, 75–244 mm TL. HAWAIIAN ISLANDS: Pearl and Hermes Reef: NMW 65106, 192 mm, holotype of *Heteromyrus atolli*. Midway Atoll: ANSP 176590, 206 mm; BPBM 34833, 3: 75–160 mm; BPBM 34878, 161 mm. JAPAN: Miyaki-Jima: BPBM 18979, 244 mm. LORD HOWE ISLAND: BPBM 14927, 293 mm; BPBM 14945, 128 mm, paratype of *Gymnothorax australicola*. RED SEA: Eilat: HUJ 15133, 203+ mm.

***Gymnothorax austrinus* n.sp.**

Southern moray

Figs. 4, 5, Pl. 1

Type material HOLOTYPE: NMV A.17858, 882 mm TL, female; Australia, Victoria, Port Philip Bay, Half Moon Bay, 37°58'S 145°01'E; F. McCoy; 1 June 1884.

Diagnosis. A large, brown moray with tapering tail; anus behind midbody, preanal length 1.8 in TL; head moderate, 8.5 in TL; depth at gill opening 18 in TL; teeth uniserial, few and highly serrated, no median intermaxillary or vomerine teeth; VF 6-68-151.

Measurements (in mm) and counts of the holotype. Total length 882; preanal length 478; head length 104; snout to dorsal-fin origin 85.6; depth at gill opening 48.5; depth at anus 41.6; snout length 19.0; length upper jaw 34.5; length lower jaw 37.0; eye diameter 6.9; interorbital width 14.0. Head pores: branchial 2; supraorbital 1 + 2; infraorbital 5; mandibular 6–7. Predorsal vertebrae 6, preanal vertebrae 68, total vertebrae 151.

Description. A large, elongate, moray with tapering tail, depth at gill opening 18, depth at anus 21 in TL; anus behind midbody, preanal length 1.9 in TL. Head moderate, its length 8.5 in TL; snout short, 5.5 in HL; jaws slightly curved and short, upper jaw 3.0 in HL. Eye above midgape, small, 15 in HL. Anterior nostril in short, small tube; posterior nostril above and before eye, small, with slightly raised rim. Head pores with some variation from the usual muraenine condition; the 2 branchial pores very small and above and before gill opening; 5 infraorbital pores, the first just behind anterior nostril and the fifth below posterior margin of eye, the “extra” pore between and above the first and second; 7 mandibular pores on the left side, 6 on right side. Dorsal-fin origin before gill opening, between first and second branchial pores; gill opening a small slit at midside. Predorsal vertebrae 6, preanal vertebrae 68, total vertebrae 151.

Teeth strong and triangular, highly serrate, upper jaw teeth very few. Five stout intermaxillary teeth continuous with 5–7 maxillary teeth, the anterior teeth large and serrate on both margins and with posterior basal knob, becoming smaller posteriorly. No median intermaxillary teeth and none on vomer. Sixteen teeth on each side of lower jaw, large and serrate anteriorly, tapering in size posteriorly.



Figure 4. *Gymnothorax austrinus*; NMV A.17858, 882 mm TL, holotype, Port Philip Bay, Victoria, Australia; diagram of head; line = 10 mm.

Overall colour medium brown, with fine dark striations in folds of skin; abdomen pale. Snout and lower jaw dark, top of head dark with darker mottling between eyes; anterior 3–4 jaw pores pale, branchial pores with faint brown rims. Very narrow pale margin on all fins, that of dorsal fin faint anteriorly.

Remarks. The single 882 mm specimen was collected many years ago off the southern coast of Victoria, Australia; it is a ripe female with ≈ 1 mm eggs. It first appeared to be similar to a large specimen of *Gymnothorax prasinus*, also taken off Victoria, but it has a much more elongate and tapering body, the anterior head region is noticeably dark, and a narrow pale margin is visible on the fins. In addition, it has much different dentition, the teeth few and highly serrate, and the vertebral count is unusual and can be matched with no known species.

Etymology. From the Latin *austrinus* “southern”. To be treated as an adjective.

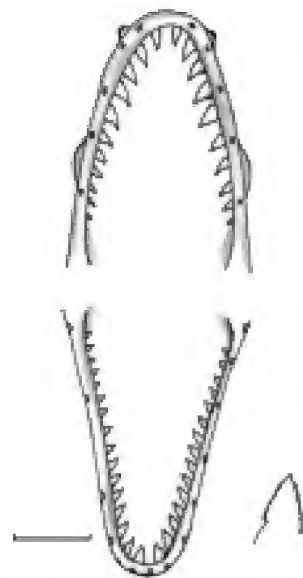


Figure 5. *Gymnothorax austrinus*; NMV A.17858, 882 mm TL, holotype; diagram of dentition; inset diagram of serrate tooth; line = 10 mm.

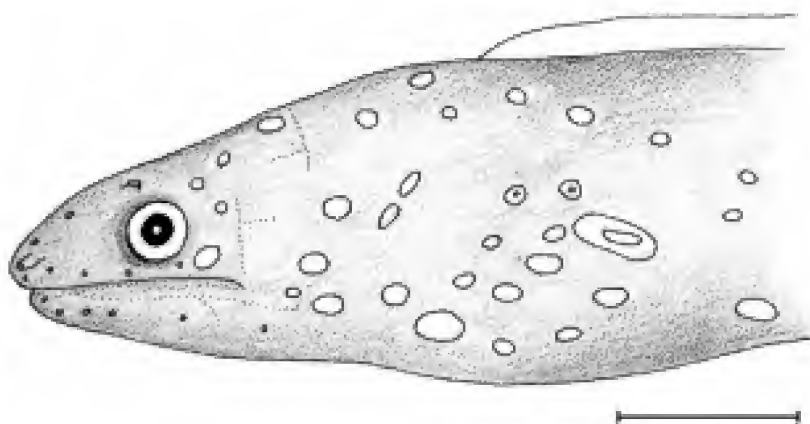


Figure 6. *Gymnothorax cephalospilus*; CAS 212449, 154 mm TL, paratype, off Port Macquarie, NSW, Australia; diagram of head; line = 10 mm.

***Gymnothorax cephalospilus* n.sp.**

Head-spot moray

Figs. 6, 7; Pl. 1

Gymnothorax sp. 4. Sainsbury *et al.*, 1984: 331.

Type material HOLOTYPE: AMS I.37982.001, 171 mm TL; Australia, NSW, off Port Macquarie, 31°16'S 153°10'E, lobster trap at 134 m; K. Graham on the FV *San Simeon*; 18 June 1999. PARATYPES (3): ANSP 177865, 159 mm, and CAS 212449, 154 mm; same data as holotype. CSIRO CA2928, 202 mm; Western Australia, N of Dampier Archipelago, 19°25'S 116°38'E, 125 m; 17 Aug. 1982.

Diagnosis. A small, slender, dark brown moray with contrasting eye-sized white spots on head; spots fewer toward anus, very few or lacking on tail; anus at midbody, preanal length 2.0 in TL; depth at gill opening 18–22 in TL; head 8.2–9.3 in TL; teeth stout, no long canines; MVF 6-64-145.

Measurements (in mm) and counts of the holotype: total length 171; preanal length 85; head length 20.7; snout to dorsal-fin origin 18.2; depth at gill opening 9.3; depth at anus 6.5; length upper jaw 7.1; length lower jaw 6.9; snout length 3.4; eye diameter 2.2; interorbital width 2.5. Head pores: branchial 2; supraorbital 1 + 2; infraorbital 4; mandibular 6. Teeth: outer intermaxillary 7–7, median intermaxillary 2; inner maxillary 3–4, outer maxillary 9; vomerine 6; dentary 14–16 + 3–5 outer teeth. Predorsal vertebrae 5, preanal vertebrae 64, total vertebrae 146.

Description. A small, slender moray, depth at gill opening 18–22 and depth at anus 26–29 in TL; anus at midbody, preanal length 2.0 in TL. Head moderate, 8.2–9.3 in TL; snout moderate, 5.2–6.1 in HL; jaws moderate, upper jaw 2.6–3.2 in HL; eye above gape, closer to rictus than to snout tip, its diameter 9.3–11 in HL. Lips papillose. Anterior nostril in moderate tube just reaching edge of jaw; posterior nostril above and before eye, with slightly raised, crenulate margin. Head pores typical (the second supraorbital pore

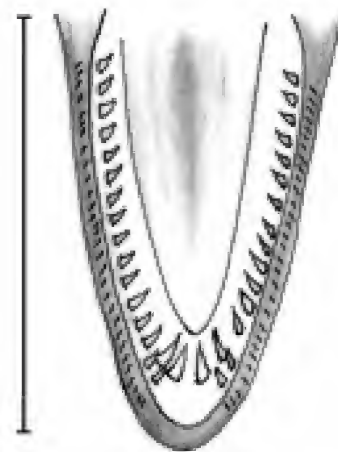
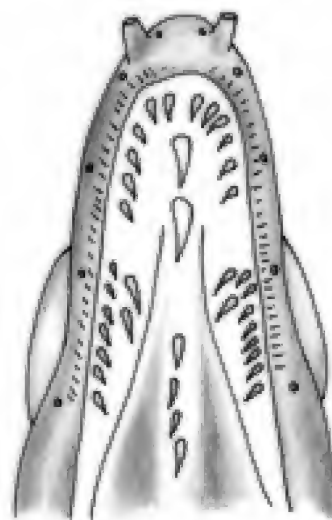


Figure 7. *Gymnothorax cephalospilus*; CAS 212449, 154 mm TL, paratype; diagram of dentition; line = 10 mm.

double on one side of one specimen), 2 branchial pores above and before gill opening. Dorsal-fin origin above second pore, closer to gill opening than to rictus. Gill opening a small slit at midside. Predorsal vertebrae 5–7, preanal vertebrae 63–65, total vertebrae 142–146; MVF 6-64-145 (4).

Teeth stout, no long canines. Peripheral intermaxillary teeth 6–8, the posterior 3 increasingly larger (the last teeth in the largest specimen with a “rough” edge posteriorly, suggesting that larger specimens may develop serrate teeth); 2 short stout median teeth. Short anterior inner row of 2–3 long slender maxillary teeth, outer row of 8–12 short triangular teeth. Single row of 5–8 short vomerine teeth. Dentary teeth in one row of 13–16 teeth, the anterior 2–5 largest and flanked with 1–5 smaller outer teeth.

Dark brown with contrasting bright white margins on fins and white spots that are numerous on head, fewer and in about 2 rows dorsally between head and anus, and lacking or only very few dorsal spots on tail. Fine lines of pale papillae outline posterior nostril and head canals; all head pores with white rims; gill opening and anus sometimes pale.

Dorsal fin dark basally, anal fin dark or with body colour basally, both fins with bright white margins for entire extent. The single specimen collected in 1982 has faded to medium brown with pale spots on head and anterior body, fin margins pale, and lines of head papillae are only faintly visible.

Remarks. All known specimens are small, the largest is 202 mm TL. The gonads of all are immature, indicating it probably grows to larger size. It is known from two collections off eastern and western Australia, both from deep waters of 125–134 m (one collection from a lobster trap). Its scarcity in collections is probably due to limited collecting in its deep-water habitat and to its small size.

These specimens differ from all known morays in their dark brown coloration with contrasting spotted head and bright fin margins, and in vertebral formula.

Etymology. From the Greek *kephale*, “head”, and *spilos*, “spot”. To be treated as a noun in apposition.

Gymnothorax cribroris Whitley, 1932a

Sieved moray

Fig. 8

Gymnothorax cribroris Whitley, 1932a: 330, pl. 39 (fig. 2). Holotype AMS IA.5012, 260 (252) mm TL; Northwest Islet, Capricorn Group, Queensland, Australia; G.P. Whitley; May 1931.

Description. A moderately large, elongate moray with tapering tail; depth at gill opening 15–20, depth at anus 15–21 in TL; anus before midbody, preanal length 2.1–2.3

in TL. Head moderately elongate, 7.3–8.6 in TL; snout 4.9–6.2 and upper jaw 2.4–2.9 in HL. Eye moderately large, 8.4–10 in HL, above midgape. Anterior nostril in long tube; posterior nostril with rim, above and behind anterior margin of eye. Head pores typical; two branchial pores above and before gill opening; dorsal-fin origin above first pore. Gill opening at midside. Predorsal vertebrae 3–6, preanal vertebrae 48–51, total vertebrae 116–125; MVF 4-50-120 (11).

Teeth strong and smooth, uniserial in adults. Peripheral intermaxillary teeth 5–6, with 1–4 tiny teeth between posterior teeth; usually 3 long median fangs. Maxilla with inner row of 1–3 long slender teeth in specimens less than 300 mm, plus outer row of 9–14 smaller teeth, becoming smaller posteriorly; single row of 9–11 teeth in large specimens. Vomerine teeth 6–14 in single row. On dentary of small specimens 2–4 large inner teeth enclosed by 3–6 small outer teeth continuing as row of 12–23 progressively smaller teeth; a single row of 13–16 teeth in large specimens.

Overall pattern of pale spots and blotches separated by brown reticulations; small pale spots on head, becoming lichenous or snowflake-like on body and tail; occiput conspicuously marked with several rows of larger dark brown spots. Lower jaw and thorax uniformly pale or with faint pattern; mouth angle and gill opening dusky; anterior nostril dark, posterior nostril with dark rim. Dorsal fin patterned, becoming dark posteriorly, with pale margin near tip of tail; anal fin patterned basally, with pale margin for entire extent. Color photographs (Sainsbury *et al.*, 1984: 55; Randall *et al.*, 1997: 36; Kuiter, 1997: 31) show dark brown spots and reticulations, the background and snowflake pattern yellowish-tan.

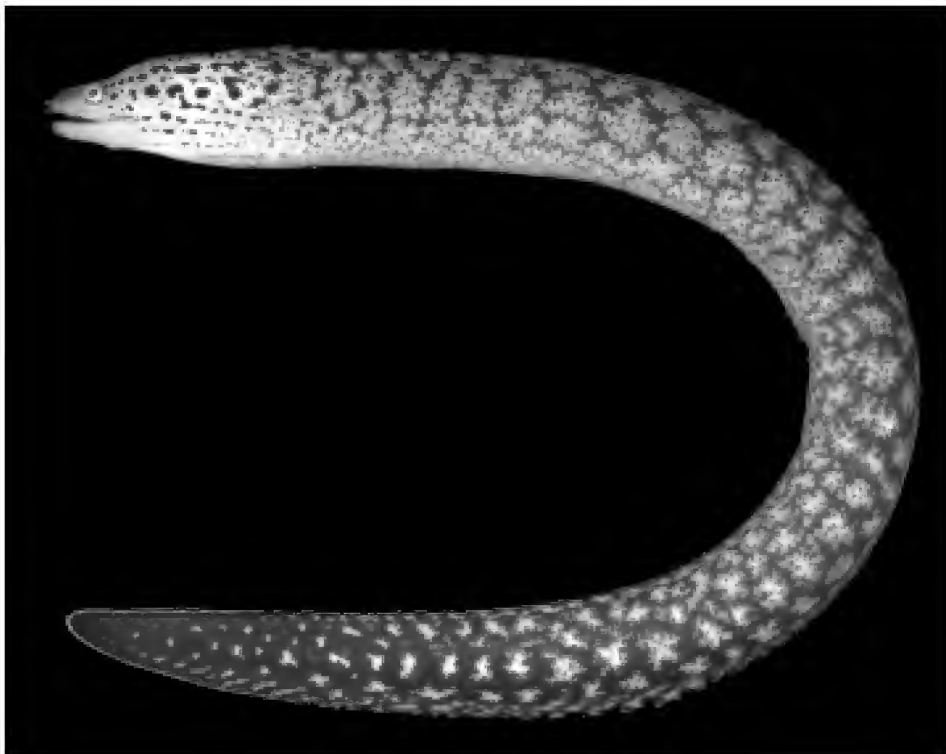


Figure 8. *Gymnothorax cribroris*; BPBM, 343 mm TL; One Tree Island; photo by J.E. Randall



Plate 1. Upper left: *Gymnothorax austrinus*, NMV A.17858, 882 mm TL, holotype; Victoria, Australia. Upper right: *Gymnothorax cephalospilus*, AMS I.37982.001, 171 mm TL, holotype; New South Wales, Australia. Lower left: *Gymnothorax longinquus*; AMS I.21943.017, 490 mm; Arafura Sea; photo courtesy of A. Graham. Lower right: *Gymnothorax obesus*; AMS IA.2658, 730 mm; paratype of *Uropterygius obesus*; off Montague Island, NSW, Australia.

Notes on holotype. The holotype of *Gymnothorax cribroris* is in fair condition, moderately small, exhibiting coloration as described above. Head pores typical except 3 branchial pores on left side. Preanal length 2.1 in TL; VF 4-51-116. Teeth strong and smooth, typical juvenile dentition; 3 rows intermaxillary teeth, median row of 3 fangs; maxillary and dentary teeth biserial anteriorly; vomerine teeth uniserial.

Remarks. The largest specimen we examined is 460 mm; none of the specimens was mature. It is taken off the east coast of Australia, from the Great Barrier Reef to Sydney Harbour, at shallow depths and often in tidepools. It is also reported from western Australia (Sainsbury *et al.*, 1984: 55; Gloerfelt-Tarp & Kailola, 1984: 54; Randall *et al.*, 1997: 36).

The overall “snowflake” or lichenous colour pattern of this species is similar to a number of other species. *Gymnothorax cribroris* is characterised and separated from the others by the distinctive dark brown spots on the side of the head and by the low vertebral count. It might be confused with *G. margaritophorus* that also has dark head spots, but which are consistently in three rows of elongate spots that radiate back from the eye, and that has a higher vertebral count (MVF 6-50-129).

Study material. Twenty specimens, 112–457 mm TL. AUSTRALIA: Queensland: AMS IA.4619, 334 mm, paratype of *Gymnothorax cribroris*; AMS IA 5012, 252 mm, holotype

of *G. cribroris*; AMS IA.5027, 233 mm, paratype of *G. cribroris*; AMS I.12629, 334 mm; AMS I.20209–021, 333 mm; AMS I.20463–020, 3: 390–410 mm; AMS I.20581–002, 133 mm; AMS I.20214.016, 201 mm; AMS I.36385–002, 457 mm; BPBM 14365, 3: 267–343 mm; CAS 87880, 2: 283–401 mm. New South Wales: AMS I.19103–044, 2: 112–230 mm; AMS I.23379–024, 343 mm; AMS I.23463.201, 409 mm.

Gymnothorax longinquus (Whitley, 1948)

Long moray

Pl. 1

Lycodontis longinquus Whitley, 1948: 73 (holotype AMS IA.6953, 720 (736) mm TL; type locality north of McKay, Queensland, Australia).

Gymnothorax sp. 1. Sainsbury *et al.*, 1984: 54 (northern Australia). *Gymnothorax* sp. 1. Gloerfelt-Tarp & Kailola, 1984: 54.

Description. A moderately large, elongate moray with tapering tail; depth at gill opening 15–24, depth at anus 18–27 in TL; anus near midbody, preanal length 2.0. Head moderately elongate, 7.2–8.7 in TL; snout short, 2.5–6.9 in HL; upper jaw moderate, 2.4–2.9 in HL. Eye above midgape, 9.4–10 in HL. Anterior nostril in short tube; posterior nostril with raised rim, above and behind anterior margin of eye. Head pores typical, (except 1 branchial pore



Plate 2. Upper left: *Gymnothorax prasinus*; WAM P.27112.001, 299 mm TL; Jervis Bay, NSW, Australia; photo by J.B. Hutchins. Upper right: *Gymnothorax prasinus*; Sydney, NSW, Australia; photo by R.H. Kuiter. Lower left: *Gymnothorax prionodon*; aquarium photograph; photo by R.H. Kuiter. Lower right: *Gymnothorax woodwardi*; Kalbarri, Western Australia; photo by J.B. Hutchins.

visible on holotype, and holotype and one other specimen have 7 mandibular pores); two branchial pores above and before gill opening, dorsal-fin origin above first pore. Gill opening at midside. Predorsal vertebrae 5–6, preanal vertebrae 59–61, total vertebrae 129–137; MVF 5-60-133 (6).

Teeth strong and smooth, uniserial in adults. Outer intermaxillary teeth 5–6, 3 long median fangs. Maxillary teeth 10–16, the first 4 increasing in size, then tapering posteriorly; inner row of 1–3 long slender teeth in specimens smaller than 350 mm. Vomerine teeth 1–7, short and sometimes hidden. Dentary teeth in single row of 15–21, the anterior 4 large, then abruptly smaller, not decreasing in size posteriorly.

Overall coloration very dark, with scattered indistinct grayish blotches on body; head paler, tail progressively darker; fins dark, with black margin. Anterior nostril with dark tip, posterior nostril with brown rim; head pores with fine brown rims. A colour photograph (Sainsbury *et al.*, 1984: 55) shows a dark brown background with paler mottlings that were said to be gray or cream.

Notes on holotype. The holotype of *Lycodontis longinquus* is a large specimen (its total length, 736 mm, is longer than Whitley's reported 720 mm). It is dark and stiff with a tag through the eye, but otherwise it is in good condition, with coloration as described above. Head pores atypical, with one branchial pore and seven mandibular pores on each side. Preanal length 2.0 in TL; VF 5-59-134. Teeth strong

and triangular; 3 rows intermaxillary teeth, 3 long fangs in median row; maxillary and dentary teeth uniserial (many missing); 1 short tooth visible on vomer.

Remarks. This species has not been identified since its description; it is here recognised as a valid species, characterised by its dark coloration and distinctive vertebral count. It is known from only a few specimens, the largest the 736 mm holotype. No mature specimens have been identified. It has been taken from scattered locations off northern Australia (from the Kimberly Region, Timor Sea, Arafura Sea, and the Gulf of Carpentaria) and from Queensland, and one specimen from a Thailand fish market (exact locality of capture uncertain). It is possibly a deep-water species (although one depth record is of 0.1–0.5 m). In addition, in all preserved specimens including the holotype, the muscles are unevenly contracted, giving a curious “lumpy” surface to the body rather than the usual smooth convex appearance of morays.

Study material. Eight specimens, 258–736 mm TL. AUSTRALIA: Queensland (“north of Mackay”); AMS IA.6953, 736 mm, holotype of *Lycodontis longinquus*. Gulf of Carpentaria: CSIRO C1408, 620 mm. Northern Territory: AMS I.21943–017, 490 mm; CSIRO T427, 344 mm; USNM 174039, 350 mm. Western Australia: WAM P.30319.106, 2: 258–299 mm. THAILAND (fish market): URM-P 12450, 619 mm.



Figure 9. *Gymnothorax nubilus*; BPBM, 535 mm TL; Lord Howe Island; photo by J.E. Randall.

***Gymnothorax nubilus* (Richardson, 1848)**

Cloudy moray

Fig. 9

Muraena nubila Richardson, 1848: 81, pl. 46 (figs. 6–10) (Holotype BMNH 1972.1.26.159; type locality Norfolk Island).
Muraena euptera Günther, 1870: 122 (holotype BMNH 1855.8.16.50; type locality Raoul Island, Kermadec Islands).

Description. A moderately elongate moray, depth at gill opening 12–22 and depth at anus 14–22 in TL; anus before midbody, preanal length 2.1–2.3 in TL. Head moderately elongate, 7.1–8.7 in TL; snout long and narrow, 4.7–5.7 in HL; upper jaw 2.5–2.8 in HL, lips papillose. Eye moderate, 9.3–13 in HL, above midgape and slightly closer to rictus than to snout tip. Anterior nostril in long tube; posterior nostril a pore above and behind anterior margin of eye. Head pores typical; 2 branchial pores above and before gill opening; dorsal-fin origin before first pore, closer to rictus than to gill opening. Gill opening at midside. Predorsal vertebrae 3–4, preanal vertebrae 50–54, total vertebrae 130–134; MVF 4-52-132 (13).

Teeth large and smooth, uniserial in adults. Outer intermaxillary teeth 6–7 plus 3–5 tiny teeth between; 3 long median fangs (none in 680 mm specimen). Maxillary teeth 11–16 in main row, the first 3–4 increasing in size, then decreasing posteriorly; small specimens (to 350 mm) with inner row of 1–3 long slender teeth. Vomerine teeth short, uniserial or slightly staggered, 5–14 (missing or hidden in largest specimens). Main row of 14–21 teeth on dentary, large anteriorly, then decreasing slightly in size; the anterior

4 teeth of some specimens (juveniles and females) form an inner row with the anterior outer 4–8 teeth smaller; a single row of dentary teeth in specimens >550 mm.

Overall coloration pale tan, with large, diffuse pale brown spots in irregular rows along base of dorsal fin and along midside, sometimes forming irregular bars on tail. Head pale tan, lower jaw, thorax and abdomen paler; head papillae in very fine brown spots forming lines on snout and top of head (similar to those marking *Gymnothorax griseus* [Lacepède, 1803] and *G. castlei* Böhlke & Randall, 2000, but not dark and contrasting); faint dark spots mark anterior lateral-line papillae (extending to gill opening and almost to anus in some specimens). Anterior nostril brown, posterior nostril with brown rim, jaw pores in faint brown rings (not visible on pale specimens). Mouth angle dusky; dark or dusky gular streaks; gill opening dusky in some specimens. Dorsal fin patterned or dusky basally, with pale margin for entire extent or only posteriorly; anal fin dusky or dark basally with noticeable pale margin. Some specimens appear uniform medium brown due to heavy mucus, only the faint dark head spots and pale margin of the fins observable.

Notes on holotypes. The holotype of *Muraena nubila* is faded but has a discernible colour pattern typical of the species as described above; the lines of spots outlining the head papillae are not visible, however Richardson's figure 7 (dorsal view of the head) shows the lines of spots. Preanal length 2.2 in TL; VF 3-52-132. Teeth large and smooth; intermaxillary teeth in 3 rows, 3 long fangs in median row; maxillary and vomerine teeth uniserial; dentary teeth biserial anteriorly.

The holotype of *Muraena euptera* is large and faded, otherwise it is in good condition; no overall colour pattern is visible, but dark gular folds and mouth angle can be seen, and there is a pale margin on the posterior dorsal fin and along the entire anal fin. Preanal length 2.1 in TL; VF 4-52-134. Teeth large and smooth; intermaxillary teeth in 3 rows, 2 long teeth in median row; maxillary dentary, and vomerine teeth uniserial. The species has seldom, if ever, been treated since its description. The holotype fits the description of *G. nubilus*, its proportions, vertebral count, tooth counts, and what remains of its colour pattern agree.

Remarks. *Gymnothorax nubilus* is said to reach 680 mm. We did not find any mature specimens. It is known from a few specimens from Norfolk Island and the Kermadec Islands, and from New Zealand, all south of 28°S. It was collected with rotenone at 0–15 m.

The general colour pattern is somewhat similar to several other species. *Gymnothorax nubilus* is distinguished by the dark spots marking the lateral-line papillae on the head and anterior body (although the spots may be faint and easily overlooked), by the pale margin on the anal fin and posterior dorsal fin, and by its vertebral formula.

Study material. Eighteen specimens, 205–680 mm TL. NEW ZEALAND: ANSP 138635, 3: 309 ca. 590 mm. NMNZ 21594, 680 mm. NORFOLK ISLAND: AMS I.4319, 554 mm; AMS I.20268-022, 9, 253–374 mm; AMS I.20270-009, 205 mm; AMS IB.5355, ca.430 mm; BMNH 1872.1.26.159, 535 mm; holotype of *Muraena nubila*. KERMADEC ISLANDS: Raoul Island; BMNH 1855.8.16.50, 604 mm, holotype of *Muraena euptera*.

Gymnothorax obesus (Whitley, 1932a)

Obese moray

Pl. 1

Uropterygius obesus Whitley, 1932a: 329, pl. 39 (fig. 1) (holotype AMS IA.3888; type locality Montague Island, New South Wales, Australia, collected in ca. 70 fms [128 m]).

Gymnothorax griffini Whitley & Phillipps, 1939: 229 (new name for specimen described as *Gymnothorax meleagris* in Griffin, 1927: 138, pl. 10, fig. 2) (holotype AIM Ps 29.1, 1020 mm TL; type locality White Island, Bay of Plenty, New Zealand).

Muraena tuhua Griffin, 1933: 171, pl. 24 (bottom), text-fig. p. 171 (holotype AIM lost; type locality 18 miles E of Mayor Island [Tuhua], New Zealand, caught on hook and line in 80 fms [146 m] by Mr McLachlan in August 1928).

Description. An elongate, very large moray, depth at gill opening 10–17 and depth at anus 15–21 in TL; anus just before midbody, preanal length 2.1–2.2 in TL. Head moderate, its length 8.5–9.2 in TL; snout 4.9–5.4 in HL; upper jaw 2.4–3.0 in HL; eye small, 12–21 in HL, above gape, closer to rictus than to snout tip. Anterior nostril in moderate tube; posterior nostril with short tube, well before eye margin. Head pores typical; two branchial pores above and before gill opening; dorsal-fin origin above gill opening and behind second branchial pore. Gill opening at midside. Predorsal vertebrae 9–10; preanal vertebrae 68–72; total vertebrae 166–172; MVF 10-70-169 (4).

Teeth smooth; maxillary teeth partially biserial. Intermaxillary teeth 5–6 plus 3–5 outer tiny teeth; 3 median teeth. Inner row of 3–5 long thin maxillary teeth, outer row of 16–17 small short teeth. Vomerine teeth up to 14, very small, pointed, hidden in muscle folds. Two to 4 large stout inner anterior dentary teeth, enclosed by 4–6 small outer teeth, continuing as row of 16–19 teeth of varying sizes. (Teeth based mostly on those of two paratypes; those of holotype and largest specimen difficult to see.)

Overall coloration of brown background with small, bright white irregular spots and semicircles. Snout uniform pale brown, without spots, lower jaw pale but mottled; coloration of uniform intensity and spotted pattern similar on all parts of body, abdomen, tail, and fins.

Notes on holotypes. The holotype of *Uropterygius obesus* is a very large, obese specimen with distinctive coloration as described above, the pattern uniform on head, body, abdomen, tail and fins. Dorsal-fin origin not obvious externally; head pores small and difficult to count. Total length described as 1515 mm, it is now approximately 1382 mm; because of its size, measurements taken are imprecise; VF 10-68-169. The mouth could not be opened to get tooth counts; Whitley reported 17 teeth on maxillaries and dentaries (the two paratypes have short anterior inner rows of maxillary and dentary teeth). Whitley described this species in the genus *Uropterygius* because the fins of the holotype are covered by flabby flesh and are not obvious externally; however, they are clearly visible in the radiograph, and can be seen externally on the two smaller paratypes.

The holotype of *Gymnothorax griffini*, AIM PS.29.1, is presumably in the collection at Auckland (not seen, inaccessible at present). A large specimen of 1020 mm TL, it was described by Griffin in 1927 under the name *Gymnothorax meleagris*; Whitley & Phillipps (1939) stated that it was not the true *G. meleagris* of Shaw, gave it the name *Gymnothorax griffini*, and referred to Griffin's description and figure. The colour description and the figure strongly suggest, and other data and dentition agree, that this name is a junior synonym of *G. obesus*, as listed in Gomon *et al.* (1994: 207).

Of *Muraena tuhua*, Castle wrote (in litt, 1999): "The type could not be found, except that there is [was] a cast made." The colour was described by Griffin as "body uniform light chocolate profusely covered with pale cream spots of a great variety of sizes and forms, none of which is margined with a deeper colour." The dorsal-fin origin was said to be only slightly before the gill opening, with both fins thick and fleshy. The colour description, proportional data, tooth counts, and figure published by Griffin suggest that *Muraena tuhua* = *Gymnothorax obesus*, and it was said to be from deep water (146 m) as were the types of *obesus*. Castle wrote to us: "I am convinced that this is *obesus*."

Remarks. *Gymnothorax obesus* is known only from the holotype, two paratypes, and one additional specimen; all are large, 730–1720 mm, the 730 mm specimen is a spent female. They were taken from temperate waters of southern Australia and New Zealand south of 35°S; the type specimens were taken in 73–128 m on the continental shelf off New South Wales

and Victoria, and the fourth specimen from North Island, New Zealand, by hook and line in 128 m. Whitley mentioned in the original description: "A living specimen in Taronga Park Aquarium, Sydney, lies with the head protruding from a heap of rocks in the usual moray fashion."

This is a valid species with an unusual colour pattern of odd-shaped, distinct small white spots on a brown background (as depicted in Whitley's figure) that is unlike and not to be confused with that of any other species.

Study material. Four specimens, 730–1720 mm TL. AUSTRALIA: New South Wales: AMS IA.3888, 1382 mm TL, holotype of *Uropterygius obesus*; AMS IA.2658, 730 mm, paratype of *U. obesus*. VICTORIA: AMS IA.4072, 860 mm, paratype of *U. obesus*. NEW ZEALAND: Poor Knight's Islands: NMNZ P.5492, 1720 mm.

Gymnothorax porphyreus (Guichenot, 1848)

Lowfin moray

Fig. 10

Muraenophis porphyreus Guichenot in Gay, 1848: 342, pl. 11 (fig. 2) (no type known; type locality Juan Fernandez Island, Chile).

Muraena chilensis Günther, 1871: 674 (holotype BMNH 1871.9.13.881; type locality Chile).

Gymnothorax Wieneri Sauvage, 1883: 161 (2 syntypes, MNHN 4868; type locality Chile or Peru).

Gymnothorax obscurirostris Rendahl, 1921: 62 (holotype NRM 7103; type locality Easter Island).

Description. A large moray, elongate when small, large specimens stout, depth at gill opening 12–20 and depth at anus 13–30 in TL; anus near midbody, preanal length 1.9–2.3 in TL. Head moderate to short, its length 7.3–10.5 in TL; snout short and broad, 4.6–6.1 in HL; jaws moderate, upper jaw 2.0–3.0 in HL. Eye above midgape, slightly closer to rictus, 9.7–19 in HL. Anterior nostril in short tube; posterior nostril above and before eye, raised or in short tube with flared crenulate margin. One (925 mm) specimen with ridge of 4 small rounded flap-like projections on nape between eyes. Head pores typical; 2 branchial pores, the second pore just above gill opening; dorsal-fin origin above or before first pore. Gill opening a diagonal slit at midside. Predorsal vertebrae 5–8, preanal vertebrae 57–62, total vertebrae 137–144; MVF 6.59–140 (26).

Teeth strong, triangular, smooth, partially biserial, moderate in number. Main row of outer premaxillary teeth usually 6, with 3–12 small outer teeth present in both small and large specimens; usually 3 caniniform teeth on midline. Inner row of 1–6 long slender maxillary teeth anteriorly, outer row of 10–18 shorter stout teeth changing little in size. Vomerine teeth short and sharp, usually in single row of 6–12 teeth (the 925 mm specimen has 24 biserial teeth). Dentary teeth 18–27, the first 4–7 large and increasing in size, then abruptly smaller, changing little in size; outer row of 2–15 short pointed teeth flanking main row anteriorly, extending back in some specimens.

Overall colour dark grey or brown with darker mottling, head, body and fins with similar coloration; nostrils and head pores noticeably dark. Snout dark, mouth angle dark, gill opening dusky or dark, but not in a defined black blotch. Fins

of small specimens (<250 mm) with pale margin or pale posteriorly; those of larger specimens with body coloration.

Notes on types. There are no type specimens for species described by Guichenot, and his description of *Muraena porphyreus* was very brief; species' identification has long been based on his colour figure on pl. 11 (fig. 2), which depicts a reddish brown moray upon which yellow marbling and small dark brown spots are superimposed. (The dorsal-fin origin is depicted as being far behind the gill opening, and prominent external upper and lower jaw bones are visible, not characters of the species.) Although no type specimens for *Muraenophis porphyreus* are known to exist (Bauchot *et al.*, 1993), we are hesitant to designate a neotype as an end in itself.

The holotypes of *Muraena chilensis* and *Gymnothorax obscurirostris*, and the two syntypes of *Gymnothorax Wieneri* have been re-examined, and data are included in the above description; vertebral counts are 8–60–137 for *M. chilensis*], 6–59–138 for *G. obscurirostris*], and 6–62–137 and 5–60–138 for syntypes of *G. Wieneri*. Randall & McCosker (1975) placed *Gymnothorax obscurirostris* Rendahl in the synonymy of *G. porphyreus* on the basis of its described morphology and coloration, but were unable to examine the holotype. We have examined the holotype, which is in good condition, and determined that it is clearly a specimen of *G. porphyreus*.

Remarks. *Gymnothorax porphyreus* grows to a large size; our largest specimen is 1030 mm. Four of the study specimens are females (395–803 mm), the 803 mm specimen ripe with 1.4 mm eggs. None are mature males. The species frequents cool waters of the eastern Pacific off Chile and Peru and is found at Easter Island, the Kermadecs, Norfolk and Lord Howe Islands, and waters of New Zealand, all south of 25°S; it was caught by rotenone, hook and line, and spear, at shallow depths recorded to 13 m.

Gymnothorax porphyreus was treated by Randall & McCosker (1975: 23) who determined and listed its synonyms; the described species were all from the eastern Pacific, but they found no differences between specimens from that area and from Lord Howe Island. Our specimens from Norfolk Island, the Kermadec Islands and New Zealand show no differences from other *G. porphyreus*. Some of the specimens from New Zealand had been identified by various museum personnel as *G. griffini* Whitley & Phillipps, a species that we and Castle have placed in the synonymy of *G. obesus*. The identity of *G. griffini* has not been confirmed, but the description of its colour and its posterior nostril fits that of *G. obesus* rather than that of *G. porphyreus*.

The overall coloration is similar to that of *G. flavimarginatus*, which is a tropical species with the gill opening in a defined black blotch, the head pores not noticeably dark, and a pale (yellow-green) margin on the posterior fins. The overall coloration is also similar to that of *G. parini*, which is found in cool southern waters of the Indian Ocean, but that has conspicuous pale margins on the fins.

Study material. Forty-five specimens, 61–1030 mm TL. CHILE: BMNH 1871.9.13.881, 345 mm, holotype of *Muraena chilensis*. EASTER ISLAND: NRM 10986, 259 mm, holotype of *Gymnothorax obscurirostris*; CAS 24762, 210 mm. Juan Fernandez Island: ANSP 122775, 850 mm. CHILE

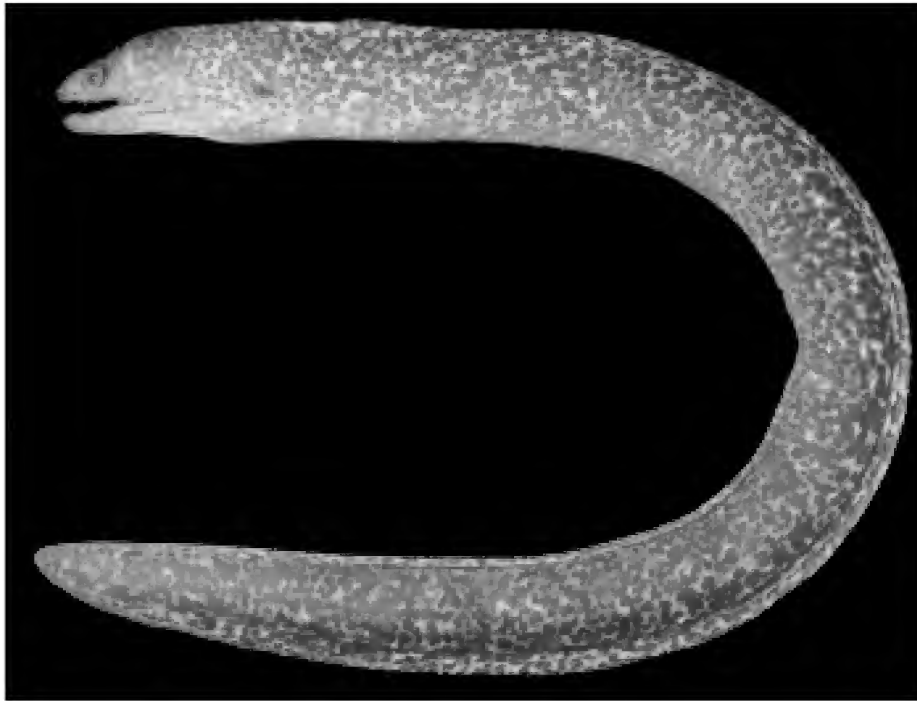


Figure 10. *Gymnothorax porphyreus*; 315 mm TL; Easter Island; photo by J.E. Randall.

or PERU: MNHN 4868, 2: 760–765 mm, syntypes of *Gymnothorax Wieneri*. PERU: Lobos de Afuera Island: SU 37399, 15: 61–400 mm. RAPA: Haurei Bay: AMNH 56170, 203 mm. NEW ZEALAND: Bay of Plenty: NMNZ 2720, 1030 mm; NMNZ 36757, 3: ca. 935–1065 mm; NMNZ 36458, 2: ca. 725–925 mm. NORFOLK ISLAND: NMNZ 26911, 760 mm. LORD HOWE ISLAND: AMS I.17368–022, 449 mm; AMS 17368–043, 2: 301–404 mm. KERMADec ISLANDS: NMNZ 4509, 595 mm; NMNZ 7019, 945 mm; NMNZ 7020, 803 mm; NMNZ 28615, 99 mm; NMNZ 28616, 3: 89–154 mm; NMNZ 35117, 202 mm; NMNZ 35144, 3: 245–403 mm; NMNZ 35150, ca. 610 mm. AUSTRALIA: New South Wales: AMS I.23379–002, 827 mm.

Gymnothorax prasinus (Richardson, 1848)

Southern green moray

Pl. 2

Muraena prasina Richardson, 1848: 93 (holotype BMNH uncatalogued; type locality Bondi Bay, Sydney, Australia).
Gymnothorax jacksoniensis Bleeker, 1863: 450 (holotype RMNH 3780; type locality Port Jackson, NSW, Australia).
Gymnothorax maculaepinnis Bleeker in Steindachner, 1866: 473 (syntypes missing; type localities Port Jackson, Macassar, Hong Kong [the latter two questionable]).
Muraena callorhyncha Günther, 1870: 122 (holotype BMNH 1861.5.18.7; type locality Freemantle, Western Australia).
Muraena krulli Hector, 1877: 468, pl. 8 (fig. 107a) (holotype lost; type locality Bay of Islands, New Zealand).
Gymnothorax leecote Scott, 1965: 54, fig. 1 (holotype QVM 1964.5.15; type locality George Rock, N of St. Helens, Cornwall, Tasmania, in crayfish net set at 10 fms.)
Verdithorax prasinus.—Whitley, 1931: 311 (new genus, orthotype *Muraena prasina* Richardson, 1848).

Notorabula callorhyncha.—Whitley, 1934: 154 (new genus, orthotype *Muraena callorhyncha* Günther, 1870).

Description. A large, elongate moray with tapering tail, depth at gill opening 12–20 and depth at anus 15–23 in TL; anus usually near or before midbody, preanal length 1.9–2.2. Head short, 8.0–10 in TL; snout moderately short, its length 5.0–6.4 in HL; upper jaw moderate, 2.4–3.0 in HL; eye small 10–15 in HL, above midgape. Anterior nostril in moderate to long tube; posterior nostril above and behind anterior margin of eye, raised or in short tube with crenulate rim. Head pores typical; 2 branchial pores, second pore just above gill opening; dorsal-fin origin above first pore, closer to gill opening than to rictus. Predorsal vertebrae 4–7, preanal vertebrae 56–60, total vertebrae 134–140; MVF 5–58–137 (16).

Teeth stout and smooth; maxillary teeth biserial anteriorly. Main intermaxillary teeth 7–10, plus 1–6 small outer teeth; 3 stout median teeth. Short inner row of 2–6 (usually 3–4) moderately long maxillary teeth in specimens of all sizes; outer row of 10–18 moderate teeth. Vomerine teeth 9–14, small and usually uniserial (19 were counted in the holotype, the first 11 teeth biserial, possibly an artifact of preservation). Usually 4 large inner dentary teeth, outer row of 19–25 teeth, the anterior 3–6 small and enclosing the large teeth.

Body and fins dark brown, usually covered with pale (greenish) mucus. Head pale brown, with median dorsal pale streak bordered on each side by dark brown streak from snout to behind eye. Nostrils and head pores dark, contrasting with head coloration; anterior nostril dark around base, posterior nostril dark brown; head pores dark, sometimes with white rims bordered by dark brown pigment. Fins dark, tip of tail sometimes pale. In life, body colour brown to dirty yellow to green; green colour may be due in part to a heavy mucous coating.

Notes on types. *Muraena prasina* was described from a “dried skin” of 23.5 inches, collected by a Mr McGillivray, and from notes made at the time of capture. The holotype was located in 1995 in the BMNH dry collection; the head and the skin of the left side had been mounted on a strip of wood, so that it appeared to be a whole stuffed specimen; the base was labelled *Muraena afra* (Günther’s identification), but the original name and locality were pencilled on the bottom of the stand. It is dark overall, with no visible pattern, the anus not discernible (the anal fin had been removed). Teeth are in good condition and countable (but many are missing); apparently 3 rows of intermaxillary teeth, 3 long median fangs; uniserial maxillary teeth (plus one inner tooth); Vomerine teeth numerous and partially biserial; dentary teeth biserial.

The holotype of *Gymnothorax jacksoniensis* was received from the Australian Museum. It is a large dark specimen with black nostrils and black head pores, and has the dorsal and anal fins dissected for their entire length, as is characteristic of many Bleeker moray types. Preanal length 1.9 in TL; VF 5-58-134. Intermaxillary teeth in 3 rows, median row of 3; maxillary and dentary teeth biserial anteriorly; vomerine teeth uniserial. Günther included this species under his catch-all listing of *Muraena afra* (an eastern Atlantic species); it has more recently been included in the synonymy of *Gymnothorax prasinus* by Paxton *et al.* (1989: 131).

Gymnothorax maculaepinnis was named in a paper by Steindachner on the fishes of Port Jackson. It listed three specimens of the moray from Port Jackson, Macassar and Hong Kong, which were presumably in the Vienna Museum at the time. The brief account followed the listing of *G. prasinus*; the single difference mentioned was that this species possessed a second row of 1–3 palatine teeth. A search was made at NMW in 1997 for specimens labelled as *G. maculaepinnis* or as *G. prasinus*, but none were found under either of those names; the types are considered to be missing. The inclusion of the species in the synonymy of *Gymnothorax prasinus* seems justified (for the Port Jackson specimen), since the two species were separated only by differences in the palatine (maxillary) teeth, a variation common in morays.

The holotype of *Muraena callorhyncha* is dark, with a median pale streak bordered by brown bands on each side which extend from the snout tip to the eye, and it has dark head pores. Dorsal-fin origin behind gill opening; preanal length 2.0 in TL; VF 11-60-137. Intermaxillary teeth in 3 rows, median row of 3 teeth; maxillary and dentary teeth biserial anteriorly; vomerine teeth not seen. The holotype exhibits the characters of *G. prasinus* except for the origin of the dorsal fin; it is placed in the synonymy of *G. prasinus*, as listed in Paxton *et al.* (1989: 131), the dorsal-fin origin considered to be anomalous.

The holotype of *Muraena krulli* “with little doubt does not exist, along with many of Hector’s types” (Castle, in litt., 1999). The “31.5 inch” specimen was briefly described as uniform dark brown without any light or dark markings, and illustrated by a line drawing. It was put in the synonymy of *Gymnothorax prasinus* by Griffin (1926: 539), who presumably had access to the holotype at the time; the name remains there.

The holotype of *Gymnothorax leecote* Scott (1965) is in the Queen Victoria Museum, Launceston, Tasmania, and was examined by the junior author. The 808 mm TL specimen

(original number 123) is identifiable as a specimen of *G. prasinus*. It is dark brown and has the dentition, morphometry, and vertebral formula (5-59-138) appropriate for the species.

Remarks. The largest specimen we examined is 855 mm; none of the specimens is mature. It is a well-known species in the south temperate waters of Australia and New Zealand, and is said to be common off New Zealand, southeastern and southwestern Australia, and taken at depths to 40 m. (A specimen of *G. prasinus* reported from Cape Radstock in far western South Australia [Glover & Branden, 1983] is presumed to have been extralimital [Hutchins, 1994: 59].) It is readily recognised by its uniform brown coloration (in preservative) with contrasting snout streak, dark nostrils and head pores. It is commonly known as the “Green moray” in Australia and the “Yellow moray” in New Zealand. We propose that it be commonly known as the “Southern green moray” so as to avoid confusion with the Green moray of the Caribbean (*G. funebris*) and the Green or Chestnut moray of the eastern Pacific (*G. castaneus*).

Whitley (1931), without explanation, described the new genus *Verdithorax* to include *Muraena prasina* and *M. krulli*. It was soon synonymised with *Gymnothorax*. Whitley (1934), with minor explanation, described *Notorabula* to include *Muraena callorhyncha*, based on Ogilby’s (1907) placement of that species in *Rabula*, a genus where it also did not belong. *Notorabula*, like *Verdithorax*, was soon synonymised with *Gymnothorax*.

Study material. Thirty-nine specimens, 155–855 mm TL. NEW ZEALAND: NMNZ 33986, 790 mm. AUSTRALIA: New South Wales: AMS I.16237–013, 326 mm; AMS I.16250–026, 304 mm; AMS I.16861–013, 483 mm; AMS I.19943–020, 299 mm; AMS I.21774–034, 2: 173–583 mm; AMS I.28738–024, 6: 280–700 mm; AMS I.31124–006, 6: 70–304 mm; ANSP 135449, 3: 142–338 mm; ANSP 138735, 8: 222–450 mm; BMNH uncatalogued, ca.610 mm (mounted half-skin), holotype of *Muraena prasina*; CAS 87884, 2: 350–446 mm; NMW 61526, 2; RMNH 3780, 572 mm, holotype of *Gymnothorax jacksoniensis*. Victoria: NMV R.8085, 855 mm. Western Australia: BMNH 1861.5.18.7, 476 mm, holotype of *Muraena callorhyncha*. Tasmania: QVM 1964: 5: 0015, 815 mm, holotype of *Gymnothorax leecote*.

Gymnothorax prionodon Ogilby, 1895

Indo-Pacific spotted moray

Pl. 2

Gymnothorax prionodon Ogilby, 1895: 720 (holotype AMS I.3324, in the Old Collection of Australian fishes; type locality Port Jackson, NSW).

Muraena mierszowskii Steindachner, 1896: 222 (holotype NMW 61642; type locality Kobe, Hiogo and Nagasaki, Japan).

Gymnothorax leucostigma Jordan & Richardson, 1909: 174, pl. 68 (holotype FMNH 52124; type locality Takao, Formosa).

Gymnothorax nirosus Tanaka, 1918: 51 (holotype ZUMT 8628 [lost]; type locality Nagasaki Fish Market, Japan).

Muraena shirleyi Griffin, 1933: 172, pl. 24 (top), text-fig. p. 173 (holotype AIM Ps.289.1, type locality Mokohinau Islands, New Zealand).

Lycodontis wooliensis Whitley, 1968: 33, pl. 8 (fig. 1) (holotype AMS IB.7941; type locality off Woolli, 29°52'S 153°20'E, NSW,

Australia, trapped in deep water).
Serranguilla prionodon.—Whitley & Phillipps, 1939: 228 (new genus,
 type species *Gymnothorax prionodon* Ogilby, 1895).

Description. A large moray with tapering tail; depth at gill opening 11–17 and depth at anus 13–21 in TL; anus before midbody, preanal length 2.0–2.2. Head elongate, 6.8–8.0 in TL; snout long and narrow, its length 4.6–6.8 in TL, head bulbous behind; jaws long, upper jaw length 2.1–3.0 in HL. Eye small, above midgape, its diameter 10–14 in HL. Anterior nostril in long tube; posterior nostril above anterior margin of eye, with raised rim. Head pores typical; 2 branchial pores above and before gill opening; dorsal-fin origin above or before first branchial pore. Gill opening at midside. Predorsal vertebrae 4–7; preanal vertebrae 53–58; total vertebrae 135–142; MVF 6-54-138 (8).

Dentition uniserial; teeth smooth (not serrate), few, long and slender, frequently broken or missing. Intermaxillary teeth 6–6, 0–3 long median teeth (absent in adults). Maxillary teeth 7–15, decreasing moderately in size posteriorly. Vomerine teeth 0–8, short and hidden in muscle folds. Dentary teeth tall and slender, 11–23, decreasing in size posteriorly.

Background colour medium brown, with small to moderate pale spots, the pattern highly variable. Small spots on dorsal head, lower jaw uniform tan; thorax and abdomen spotted in large specimens. Body spots small, ocellated, and moderately separated in small specimen (the holotype), becoming larger and divided into segments in larger specimens, sometimes fewer, more widely separated, and ocellated on tail. Both dorsal and anal fins slightly dark, with 1–2 rows of spots, frequently a row on margin of fins some of which may be joined, but not forming a continuous pale margin on fins. Mouth angle and gill opening dusky; dark gular folds present. Color photos in Coleman (1983: 41) and Kuitert (1993: 33) show a reddish-brown background with small pale spots dorsally on the head, larger and extending ventrally on the body, and slightly smaller, more widely spaced, and ocellated on the tail. In the largest (866 mm) specimen from New Zealand the spots were separated and ocellated on the entire body and tail similar to the spots on the holotype.

Notes on types. The holotype of *Gymnothorax prionodon* is moderately small, in poor condition, its jaws dissected and broken. It is faded brown, with small, pale, well-spaced ocellated spots visible on the body and tail, and a row along the base of the dorsal fin. Preanal length 2.2 in TL; VF 6-58-140. Teeth mostly missing (sockets visible); the few remaining show a basal knob but are not serrate (as described by Ogilby); subsequent descriptions of the species note “None of teeth serrate” (Griffin, 1926: 538). Intermaxillary teeth in 2 outer rows, no median teeth; maxillary and dentary teeth uniserial, no vomerine teeth (a few depressions could be sockets).

The holotype of *Muraena shirleyi* was not seen by us but was previously examined by Castle (in litt., 1999) who provided its catalogue number, length (1030 mm), and VF (4-53-136?). Its proportions, counts, dentition, and colour description, as well as Griffin’s figure on plate 24 (top), indicate it is a junior synonym of *Gymnothorax prionodon*. Griffin himself said “At first sight it might be taken for a

pale variety of *G. prionodon*, but there are... differences...” Griffin had previously (1926) described a 714 mm specimen of *G. prionodon* from Mokohinau Islands (northeastern North Island, NZ).

The holotype of *Lycodontis wooliensis* is a moderately large male specimen with a tapering tail and is in good condition. It is medium brown, the head spotted dorsally, body with large, irregular pale spots which are divided into segments; dorsal fin spotted, anal fin spotted basally with darker margin (adult coloration). Total length, 773 mm (longer than Whitley’s 740 mm); preanal length 2.0 in TL; VF 6-54-142. Intermaxillary teeth in 2 outer rows, no median teeth; maxillary, vomerine, and dentary teeth uniserial.

The identity of *Gymnothorax prionodon* has not been well documented, and we found few specimens in collections. Some underwater photographs have been identified as that species (Coleman, 1983: 41; Castle, unpublished). Studies of those specimens and comparison with the holotypes of several white-spotted species described from the northwestern Pacific suggest it is conspecific with several described species, all from deep temperate waters: *Muraena mierszewska* and *Gymnothorax nirosus* from Japan, *Gymnothorax leucostigma* from Taiwan, and *Lycodontis wooliensis* from New South Wales. Holotypes of these have been recently re-examined, data recorded and included in the description above. They are all larger specimens, and have the large complex spots of adults as described above and as depicted in recent photographs of *Gymnothorax prionodon*. The holotype of *Gymnothorax mierszewska* is a large specimen with excellent colour pattern and VF of 5-54-135; that of *G. leucostigma* has a similar colour pattern and VF of 5-53-136; the holotype of *G. wooliensis* is described above. *Gymnothorax nirosus* was described in Japanese by Tanaka in 1918, and later (Tanaka, 1931: 21) listed (as *G. nivovus* [sic]) as a junior synonym of *G. mierszewska*. The holotype has been declared lost; the name is retained in the synonymy of *G. prionodon* based on Tanaka’s synonymy of *G. nirosus* with *G. mierszewska*.

Remarks. *Gymnothorax prionodon* is said to reach 1000 mm (Coleman, 1983: 41). Our largest study specimen is 866 mm; the 498 mm specimen is a developing female, the 866 mm a male. Our specimens are from moderate to deep waters (recorded 37–128 m) south of the equator, off southern Queensland and NSW on the east coast of Australia, and off New Zealand. North of the equator, it is known from off northern Taiwan and Japan.

Lycodontis johnsoni Smith, 1962, taken off the east coast of Africa and in the Red Sea, is very similar to *G. prionodon*, but there are subtle differences in adult coloration; juveniles of both have separated, ocellated pale spots, but adults of *johnsoni* have numerous closely-set white spots separated by brown reticulations. Another similar species is *G. kidako* (Temminck & Schlegel, 1846), also from the northwestern Pacific and Queensland, and the closely related *G. niphostigmus* Chen, Shao & Chen, 1996, from Japan and Taiwan; they are readily separated by the colour pattern of larger “snowflake-like” spots, a prominent pale margin on the anal fin, and more vertebrae (MVF 5-55-141 and 4-54-141 respectively).

Gymnothorax prionodon is the type species for the genus *Serranguilla* Whitley & Phillipps, the new genus that they based on Ogilby’s statement that it possessed serrate teeth,

and the common name applied to this species was the “sawtooth moray.” However, the holotype and all specimens examined do not possess serrate teeth.

Study material. Eight specimens, 315–886 mm TL. JAPAN: NMW 61642, 832 mm; holotype of *Muraena mioszewska*. TAIWAN: ANSP 176116, 2: 482–535 mm; FMNH 52124, 790 mm, holotype of *Gymnothorax leucostigma*. AUSTRALIA: New South Wales: AMS I.3324, 315 mm; holotype of *Gymnothorax prionodon*; AMS IB.7941, 773 mm, holotype of *Lycodontis wooliensis*. Queensland: QM I9153, 498 mm. NEW ZEALAND: Bay of Plenty: NMNZ 4857, 866 mm.

Gymnothorax woodwardi McCulloch, 1912

Woodward’s moray

Pl. 2

Gymnothorax woodwardi McCulloch, 1912: 80, fig. 1 (holotype WAM P.13263.001; type locality Pelsart Island, Western Australia).

Description. A moderately large moray, depth at gill opening 12–24 and depth at anus 14–23 in TL; anus before midbody, preanal length 2.1–2.3 in TL. Head 7.7–8.6 in TL; snout elongate, 4.4–5.4 in HL, upper jaw 2.0–2.6, and eye 9.3–11 in HL, slightly closer to rictus. Anterior nostril in long tube; posterior nostril a pore above anterior margin of eye. Head pores typical; 2 branchial pores above and before gill opening; dorsal-fin origin above or before first pore, closer to rictus than to gill opening. Gill opening at midside. Predorsal vertebrae 4–5; preanal vertebrae 56–58; total vertebrae 134–141; MVF 4-57-137 (5).

Teeth long and smooth, very slender and sharp, uniserial in adults. Peripheral intermaxillary teeth 6 plus 0–4 tiny teeth between, present in small specimens, not visible in specimens greater than 400 mm; 3 very long stileto-like median teeth. Maxillary teeth 9–14, decreasing in size posteriorly, plus 1–2 longer inner teeth in specimens smaller than 300 mm. Vomerine teeth 8–11, short and rounded, sometimes staggered. Main row of 12–18 dentary teeth, large anteriorly and decreasing in size posteriorly, sometimes a few tiny outer teeth anteriorly.

Body colour pale tan with brown reticulum outlining pattern of about 3 rows of large polygonal pale spots dorsally, pale and unpatterned ventrally. Head pale, with dark or dusky gular streaks and mouth angle; pale and unpatterned ventrally. Dorsal fin patterned or dusky basally, with pale margin posteriorly; anal fin dark basally with narrow pale margin. A colour photograph of a live specimen appears in Kuiter (1997: 31).

Notes on types. The holotype, WAM P.13263.001, was not seen by us; the data presented in the original description were based on the holotype and four paratypes. We examined three of the four paratypes, now at AMS, and data were taken. They have coloration similar to that depicted in figure 1 of the original description. The vertebral formulae of the three paratypes examined are: AMS I.7235, VF 4-56-134, and AMS I.12224–12225, VF 4-56-137 and 4-58-135.

Remarks. This species is fairly common off western Australia but has not been taken elsewhere. The largest known is 577 mm, but no mature specimens were seen. It inhabits offshore waters; one specimen was reported from 182 m. It is best identified by its colour pattern of pale polygons on the dorsal half of its body and by its very slender, stileto-like teeth.

Study material. Eleven specimens, 302–577 mm TL. WESTERN AUSTRALIA: CAS 87879, 245 mm. Cape Naturaliste–Geraldton: AMS E.2473, 302 mm. Houtman Abrolhos: AMS I.7235, 310 mm, paratype of *Gymnothorax woodwardi*. Nanduran: AMS IB.1635, 575 mm. Pelsart Island: AMS I.12224, 420 mm, and AMS I.12225, ca. 577 mm, paratypes of *Gymnothorax woodwardi*. Rottne Island: AMS I.20240–001, 2: 330–374 mm. Swan River: AMS I.13147, 424 mm. Perth: CAS 131886, 2: 495–575.

Notes on additional Australian and New Zealand muraenids

Type specimens

Muraena helena australiae Richardson, 1848: pl.49 (figs. 1–6). Holotype BMNH 1847.5.10.16, 25 in. (594 mm) TL; Australia.

= *Muraena helena* Linnaeus, 1758

The name *Muraena helena australiae* appears in the caption for pl. 49 following Richardson’s description of *Muraena helena* from Gibraltar; measurements are presented for the specimen from Australia (which agree with the designated holotype), and for a 30 inch specimen from Gibraltar. Counts, proportions, dentition, and vertebral counts are typical for *M. helena* from the eastern Atlantic and Mediterranean. The locality of Australia is considered to be erroneous. Supporting this is the fact that the original catalogue entry lists no locality; on the same page two other morays are listed with no locality: *M. polyzona*, known from the Indo-Pacific, and *M. pavonina*, originally described without a locality and considered by early authors (Richardson, 1848; Günther, 1870) to be from the “South Seas”, but later discovered (Böhlke *et al.*, 1989: 199) to most probably have been collected at Ascension Island in the Atlantic Ocean. Ogilby (1907: 11) unnecessarily created the replacement name *Muraena vorax* for *Muraena helena australiae* Richardson, and we include *vorax* within the synonymy of *M. helena* Linnaeus.

Muraena cancellata Richardson, 1848: 87, pl.46 (figs. 1–5). BMNH, 3 syntypes, 17.5 in. TL (not found); Western Australia, Surgeon Bynoe; Cape Upstart; Sumatra, College of Surgeons. (from Richardson).

= *Gymnothorax undulatus* (Lacepède, 1803)

None of the syntypes of *Muraena cancellata* can be located (one must have been extensively dissected to provide Richardson’s description of organs, osteology, and vertebral counts). The colour pattern described and illustrated, as well as the tooth and vertebral count of 4-50-127 given by Richardson, fit *Gymnothorax undulatus* with which it has long been synonymised.

Gymnothorax chalazius Waite, 1904: 145, pl.17, fig. 2. Holotype AMS I.5479, 415 (413) mm TL; Lord Howe Island; E.R. Waite and A.R. McCulloch.

= *Gymnothorax eurostus* (Abbott, 1861)

The holotype of *Gymnothorax chalazius* is relatively stout and of moderate size, dark brown overall, with faded but typical colour pattern of about 4 rows of dark spots dorsally, and small pale spots overall, visible on head, body and fins. Total length 413 mm; preanal length 2.3 in TL; VF 6-48-124. Teeth numerous, short and stout; intermaxillary teeth in 5 rows across with 2 in median row; maxillary and dentary teeth biserial; vomerine teeth uniserial. *Gymnothorax chalazius* was put in the synonymy of *G. eurostus* by Randall & McCosker (1975: 25); the holotype and other specimens identified as *G. chalazius* at AMS are specimens of *G. eurostus*. (AMS I.6271, 315 mm; Lord Howe Island; "Old Collection", registered before Sept. 1903, may be the paratype mentioned as "a second example... 320 mm...")

Gymnothorax dakini Whitley & Colefax, 1938: 285, pl. 14 (fig. 2). Holotype AMS IA.6990, 576 mm TL (lost); Nauru, Gilbert Islands; Prof. W.J. Dakin; 1934.

= *Gymnothorax*, *nomen dubium*

The holotype of *Gymnothorax dakini* cannot be located in the Australian Museum. It was described as a large moray, yellow brown mottled with dark, the edge of the fins pale dirty-yellow, with gill opening and mouth angle not dark. Total length 576 mm; calculated preanal length 2.4 in TL. Teeth smooth; vomerine teeth "a well developed row on each side." The proportional data, colour of the body and fins, and biserial vomerine dentition suggest that it might be *Gymnothorax flavimarginatus*, a common tropical species but which has the gill opening in a dark blotch. The name is therefore considered to be a *nomen dubium*.

Muraena elegantissima Kaup, 1856: 67. Holotype MNHN B.2466, 8.11 in. (195 mm) TL; Australia?; J.S.C. Dumont, Austrolabe Expedition; 1826–1829.

= *Gymnothorax pictus* (Ahl, 1789)

The holotype is small, shrivelled, and difficult to measure; it is pale, with 3 rows of dark spots along body, including abdomen; head and lower jaw spotted. Total length 195 mm; preanal length 2.1 in TL; VF 9-57-131. Intermaxillary teeth in 3 rows, 1 short tooth in median row; maxillary and dentary teeth uniserial; vomerine teeth staggered. Coloration, proportions, and vertebral count support its identity as *Gymnothorax pictus*.

Gymnothorax garsiae Whitley & Colefax, 1938: 286, pl. 14 (fig. 3). Holotype AMS IA.7171, 129 mm TL (lost); Gilbert Islands, on reef flat; Prof. Harvey Sutton; March 1937.

= *Gymnothorax*, *nomen dubium*

The holotype cannot be found in the Australian Museum. It was described as dark uniform brown to black, with a narrow edge of white around tip of tail. Total length 129 mm;

preanal length calculated as 2.2 in TL. Teeth long, acute fangs, largest anteriorly, an inner row of 4 maxillary teeth. This generalised description of a very small specimen provides few clues to its identity, and the name must be considered a *nomen dubium*.

Anarchias insuetus Whitley, 1932b: 272, fig. 1. Holotype AMS IA.4448; 185 mm TL; Australia, Queensland, Low Isles off Port Douglas; G.P. Whitley, Boardman.

= *Uropterygius*, *nomen dubium*

The holotype is small and completely faded with no discernible pattern; there is a large hole behind the anus. Preanal length 2.2 in TL; VF 98-104-115. Teeth numerous, long and hooked back; intermaxillary and maxillary teeth continuous, with an inner row of fewer well-spaced teeth and an outer row of many small teeth; vomerine teeth long and well-spaced; inner row of long dentary teeth, outer row mostly missing and uncountable.

This species was put in the genus *Anarchias* when it was thought that species of *Anarchias* had a long dorsal fin (found to be a fold of flesh, the fin-rays confined to the tip of the tail). It lacks the fourth supraorbital pore that defines *Anarchias*, and therefore belongs in *Uropterygius*; the species cannot be determined due to the poor condition of the holotype. Recent publications (Paxton *et al.*, 1989: 127; Eschmeyer, 1998: 780) have misspelled the species name as "*insuentus*".

Fimbrinares mosaica Whitley, 1948: 72. Holotype AMS IA.3926, 1033 (1069) mm TL; Point Banks, Botany Bay, NSW, 2 m; H. Warner; 23 June 1929.

= *Enchelycore ramosa* (Griffin, 1926)

The holotype is large and hard, measurements taken only approximate. It is dark tan with dark brown reticulations forming large squares along body and tail, the squares patterned with small brown spots; fins similarly patterned; head with diffuse pattern. Mouth not closing completely, exposing long fang-like teeth; posterior nostril above and before eye, the inside of the nostril protruding (the tassel-like fringes mentioned by Whitley which are the basis for his new genus *Fimbrinares*). Preanal length 2.2 in TL; VF 6-54-145. Teeth numerous, of varying sizes with many long fangs, mouth not closing completely. Intermaxillary teeth in 5 rows across, with 4 median teeth; about 2 rows of long fang-like inner maxillary teeth plus irregular outer row of shorter teeth of varying sizes; no vomerine teeth visible; 11 long inner dentary teeth, irregular outer row of teeth of varying sizes, none as large as those of inner row. This species was put in the synonymy of *Enchelycore ramosa* by Randall & McCosker (1975), based on coloration and dentition.

Gymnothorax ramosus Griffin, 1926: 539, pl. 94. Holotype AIM; Whangaroa and Bay of Islands, North Auckland, New Zealand.

= valid as *Enchelycore ramosa* (Griffin, 1926)

We did not see the holotype or the paratype and are unaware of recent information concerning their existence. The colour

pattern of large, spotted, polygonal spots formed by dark reticulations on head, body and fins, dorsal fin with narrow pale margin, anal fin dark basally with pale margin, is depicted on plate 94, as is the fang-like dentition. Color photographs of live *Enchelycore ramosa* appear in Randall (1970: 57) and Kuitert (1993: 33). Its identity as a valid species of *Enchelycore* was proposed by Randall & McCosker (1975) and followed by Paxton *et al.* (1989: 128).

Gymnothorax scriptus Schneider in Bloch & Schneider, 1801: 529. Holotype ZMB (missing); New Holland, Australia.

= *Gymnothorax*, *nomen dubium*

This species was briefly described in Latin only; the type specimen could not be located at ZMB (the description stated "Kaan dictus", suggesting that no specimen existed, according to H.-J. Paepke, pers. comm., 1995). The name must be considered a *nomen dubium*.

Miscellaneous remarks

During the course of this study, several names have been deleted from previously published lists of Australian species (the most recent, Paxton *et al.*, 1989) and some specimens mentioned in published accounts have been re-identified. Australian specimens identified as *Gymnothorax melanospilos* (Bleeker, 1855) (a junior synonym of *G. isingteena* [Richardson, 1845]) were incorrectly identified. Species that have now been determined to be junior synonyms include: *Anarchias fuscus* Smith, 1962 = *A. allardicei*; *Gymnothorax boschii* (Bleeker, 1853) = *Echidna nebulosa*; and *Gymnothorax woolienseis* Whitley, 1968 = *G. prionodon*. Four names are considered to be *nomen dubia*: *Anarchias insuetus* (usually cited as *A. insuentus*), *Gymnothorax dakini* and *G. garsiae* (types lost), and *G. scriptus* (type not extant); these species are not identifiable (Australian specimens previously identified as *G. scriptus* have been re-identified as *G. minor*). The locality of *Muraena australiae* Richardson, 1848, is considered to be erroneous; the type specimen is a common Mediterranean species, *M. helena*. In addition, four morays are here included in different genera (*Echidna zebra* = *Gymnomuraena zebra*; *Siderea picta* = *Gymnothorax pictus*; *Siderea thyrsioidea* = *Gymnothorax thyrsioideus*; and *Uropterygius obesus* = *Gymnothorax obesus*), and the name of one species has been changed (*Thyrsoidea macrura* = *Strophidon sathete*). The wide-ranging Indo-Pacific Zebra moray, *Gymnomuraena zebra*, was also treated by earlier authors as *Arndha zebra*. And in much of the 20th century literature, many species now recognised as *Gymnothorax* were interchangeably placed in *Lycodontis*.

We have identified the specimens from Lord Howe Island identified as "*Gymnothorax* sp." in Allen *et al.* (1976: 376–377) as follows: sp. A (AMS I.17456–001) is *G. eurostus*; sp. B (BPBM 14927) is *G. atollis*; and sp. C (BPBM 14786) is *G. javanicus*; the specimen identified as *G. panamensis* (BPBM 14945) and later described by Lavenberg (1992) as a paratype of *G. australicola* is *G. atollis*.

We have identified those photographs of morays published by Sainsbury *et al.* (1984: 55–57) and by Gloerfelt-Tarp & Kailola (1984: 54–57) as follows: *Gymnothorax* sp. 1 is *G. longinquus*; *Gymnothorax* sp. 2 is

G. pseudothyrsioideus; *Gymnothorax* sp. 3 is *G. mccoskeri*; and their *Gymnothorax reticularis* is *G. minor*. In addition, we have identified those species listed in Sainsbury *et al.* on page 331 as follows: *Gymnothorax* sp. 4 is *G. cephalospilus*; sp. 5 is *G. thyrsioideus*; sp. 6 is *G. pseudothyrsioideus*; and sp. 7 is *Uropterygius nagoensis*.

Comments on Australian/New Zealand muraenid distributions

It is safe to assume that the majority of shallow water moray species, particularly in tropical Australian waters, have been discovered. Although most moray eels normally inhabit waters shallower than 50 m, the junior author (unpublished data) recently observed from submersible dives in the eastern Pacific and western Atlantic that they tend to occupy considerably deeper reef habitats than previously thought. The recent discovery of new muraenid species is often because they come from habitats that are extremely difficult to sample except by deep trapping. And on that basis, we presume that the shallow water distribution data comprise the more reliable patterns of zoogeographic significance.

The widespread distribution of many anguilliform fishes is due in large part to their long larval life and the suitability of the leptocephalus to a planktonic existence. Little however is known about the duration of muraenid leptocephali. Castle (1965) estimated muraenid larval duration to be eight to ten months for those Indo-Pacific species he examined, whereas estimates of larval duration for the widely distributed western Atlantic *Gymnothorax ocellatus* range from six to eight months (Eldred, 1969, as *G. nigromarginatus*) to as few as three months (Smith, 1989). The majority of Australian morays (43 of 59 species) are broadly distributed across the northern tropical coast and widespread in the tropical Indo-Pacific. Of those, nine have crossed the eastern Pacific barrier (Rosenblatt *et al.*, 1972) and are occasionally found at the offshore islands of Galápagos, Cocos, and Clipperton (McCosker & Rosenblatt, 1995; McCosker & Humann, 1996), 22 extend westward as far as the African coast (Castle & McCosker, 1986), and 11 occur in the Red Sea (Randall & Golani, 1995). Three species are antitropical (*Gymnothorax kidako*, *G. minor*, and *G. prionodon*) and *G. eurostus* is antiequatorial (cf. Randall, 1982) in distribution, although their taxonomy is problematic at this time. It is likely that genetic analysis will better explain those relationships.

Three species display a temperate distribution that extends eastward to Easter Island (including *Anarchias seychellensis*, whose identity is problematic, and *Enchelycore ramosa*) and one of them, *Gymnothorax porphyreus*, is also common along the eastern Pacific mainland to Chile and Peru (Randall & McCosker, 1975). Close affinities between temperate Australia, New Zealand, and Chilean shorefishes are not uncommon (Mead, 1970; McCosker, 1970, 1971), however in most cases they are not conspecifics. Again, a comprehensive genetic comparison would help to clarify the level of interchange and similarity. Seven moray species have an Australia and New Zealand distribution limited to temperate waters south of 25°S; they include *Enchelycore ramosa*, *Gymnothorax annasona*, *G. austrinus*, *G. nubilus*, *G. obesus*, *G. porphyreus*, and *G. prasinus*. It is curious that the only moray known to inhabit

Tasmania is *G. prasinus*. We are uncertain as to the status of *G. atolli* (known from specimens of variable quality from Lord Howe Island, Japan, the northern Hawaiian archipelago, and the Red Sea) and make no firm conclusions about its taxonomic or geographic status.

Several species are endemic to Australia and New Zealand and it is likely that this is not, in most cases, an artifact of rarity in collections. (We exclude *Gymnothorax australinus*, known only from the holotype.) Species known only from northern Australia include *G. cephalospilus*, *G. cribroris*, and *G. mccoskeri*. *Gymnothorax woodwardi* is a fairly common shallow water species known only from SW Australia (Kuiter, 1997). And finally, the southern species *G. annasona* (known only from Lord Howe Island and Middleton and Elizabeth reefs) and *G. nubilus* (known from New Zealand, Norfolk Island and the Kermadec Islands) are well represented in collections but limited in distribution.

Further collecting efforts along the NW coast of Australia as well as deep trawling and trapping throughout Australian waters will likely result in the capture of additional muraenid wonders. We look forward to those discoveries.

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- obesus*, *Uropterygius* 88, 91, 92, 98
- obscurirostris*, *Gymnothorax* 92
- ocellatus*, *Gymnothorax* 98
- panamensis*, *Gymnothorax* 98
- parini*, *Gymnothorax* 84, 92
- pavonina*, *Muraena* 96
- picta*, *Siderea* 98
- pictus*, *Gymnothorax* 73, 82, 97, 98
- pindae*, *Gymnothorax* 73, 79
- polyuranodon*, *Gymnothorax* 73, 81
- polyzona*, *Echidna* 73, 76
- polyzona*, *Muraena* 96
- porphyreus*, *Gymno* 72–74, 81, **92**, 93, 98
- porphyreus*, *Muraena* 92
- porphyreus*, *Muraenophis* 92
- prasina*, *Muraena* 93, 94
- prasinus*, *G*.. 72, 73, 78, 85, 89, **93**, 94, 98, 99
- prasinus*, *Verdithorax* 93
- prionodon*, *G* 72, 73, 80, 89, **94**–96, 98
- prionodon*, *Serranguilla* 95
- pseudoherreii*, *Gymnothorax* 73, 74, 78
- pseudothyrsoideus*, *Gymnothorax* .. 73, 82, 98
- quaesita*, *Rhinomuraena* 73, 77
- Rabula* 94
- ramosa*, *Enchelycore* 73, 77, 97, 98
- ramosus*, *Gymnothorax* 97
- reticularis*, *Gymnothorax* 98
- rueppelliae*, *Gymnothorax* 73, 78
- sathete*, *Strophidon* 73, 77, 98
- scriptus*, *Gymnothorax* 74, 98
- Scuticaria* 72
- Serranguilla* 95
- seychellensis*, *Anarchias* 73, 75, 98
- shirleyi*, *Muraena* 94, 95
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- sp. 2*, *Gymnothorax* 98
- sp. 3*, *Gymnothorax* 98
- sp. 4*, *Gymnothorax* 86, 98
- sp. 5*, *Gymnothorax* 98
- sp. 6*, *Gymnothorax* 98
- sp. 7*, *Gymnothorax* 98
- sp. A*, *Gymnothorax* 84, 98
- sp. B*, *Gymnothorax* 98
- sp. C*, *Gymnothorax* 98
- Strophidon* 72
- thyrsoidea*, *Siderea* 98
- thyrsoideus*, *Gymnothorax* 73, 77, 98
- tuhua*, *Muraena* 91
- undulatus*, *Gymnothorax* 73, 81, 96
- unicolor*, *Echidna* 73, 76
- Uropterygius* 72, 74, 75, 81, 91, 97
- Verdithorax* 94
- Wieneri*, *Gymnothorax* 92, 93
- woodwardi*, *Gymno* 72, 73, 80, 89, **96**, 99
- wooliensis*, *Gymnothorax* 95, 98
- wooliensis*, *Lycodontis* 94–96
- zebra*, *Arndha* 98
- zebra*, *Echidna* 98
- zebra*, *Gymnomuraena* 73, 76, 98
- zonipectis*, *Gymnothorax* 73, 82

***Paedogobius kimurai*, a New Genus and Species of Goby (Teleostei: Gobioidae: Gobiidae) from the West Pacific**

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ABSTRACT. *Paedogobius kimurai*, a new genus and species of Gobiidae, is described. This diandric genus is unique among the Gobiidae in having a long rod-shaped pelvis separated posteriorly into distinct left and right halves and no subpelvic process; and the ectopterygoid and quadrate widely separated in the secondary male. This genus is also distinguishable from the other genera of Gobiidae in having the following combination of characters: a maxillo-vomerine meniscus; the posteriormost soft dorsal- and anal-fin pterygiophores each supporting an unbranched soft ray; 10 abdominal and 15 caudal vertebrae; the first one or two dorsal-fin pterygiophores inserting between the 9th and 10th neural spines; some sensory papillae on the branchiostegal region; and no first dorsal fin. Mature females (about 15 mm SL) have a transparent body with only a few melanophores, no pelvic fins, small jaws with a few minute teeth, and the nostrils formed into a single pit. Secondary males (about 16 mm SL) have pelvic fins, many melanophores especially on the head, and a robust head with large jaws armed with long canine-like teeth, and two nostrils. Primary males (about 12 mm SL), are smaller than females, and also have pelvic fins and two nostrils; however, the head is not robust, the small jaws are armed with a pair of short canine-like teeth and pigmentation is diffuse. This species is known from Japan, Thailand and northeastern Australia.

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The Gobioidae comprises about 270 nominal genera and 1,500–2,000 species (Hoese, 1984). Some gobioid genera have juvenile or larval-like characteristics when adult, with a transparent body and planktonic life mode. Examples of these are: the European genera *Aphia* Risso, *Crystallogobius* Gill and *Pseudaphya* Iljin; *Grahamichthys* Whitley from New Zealand; and the Indo-Pacific *Gobiopterus* Bleeker, *Leucopsarion* Hilgendorf, *Rotuma* Springer, *Mistichthys* Smith, and *Tyson* Springer. The Indo-Pacific fish *Schindleria* is perhaps the most larval-like, and is now known to be a gobioid (Johnson & Brothers, 1993). Some of these small gobioid genera form schools hovering above the substrate (such as *Gobiopterus* and *Mistichthys*).

An unusual diandric goby not belonging to any of the above-mentioned paedomorphic genera was collected from coral reef and estuarine habitats in Japan, Thailand and Australia. We herein describe this species as a new genus and species of Gobiidae.

Materials and methods

Counts and measurements follow Nakabo (1993). Measurements were taken using a binocular microscope with an ocular micrometer, read to the nearest 0.1 mm. Notation of the dorsal-fin pterygiophores and vertebrae (P–V) follows Akihito *et al.* (1984). Vertebrae were counted from cleared and stained specimens prepared following the procedure of Dingerkus & Uhler (1977).

Osteological observation were based on cleared and stained specimens. Terminology of osteology follows Gill & Hoese (1993) and Johnson & Brothers (1993). Cephalic sensory papillae were examined by staining the specimens with suminol cyanine. Catalogue abbreviations follow Leviton *et al.* (1985) except BLIH, Biological Laboratory, Imperial Household, Tokyo.

Paedogobius n.gen.

Type species. *Paedogobius kimurai* n.sp.

Diagnosis. Pelvis formed into long rod, extending posteriorly to vertical line through mid point of third abdominal vertebra. Left and right pelvic bones distinctly separated from each other posteriorly. Subpelvic process absent in both sexes. Ectopterygoid and quadrate widely separated in secondary male. Some sensory papillae present on branchiostegal membranes. Maxillo-vomerine meniscus present. First dorsal fin absent. Dorsal- and anal-fin pterygiophores each supporting one unbranched soft ray, with supernumerary ray on first pterygiophore of anal fin. Ten abdominal and fifteen caudal vertebrae. First one or two dorsal pterygiophores inserting between ninth and tenth neural spines.

Description. Data for holotype given first, followed by range and mode of paratype data in parentheses (see also Figs. 1–8 and Table 1).

Dorsal fin 14 (13–16, 14); anal fin 15 (14–15, 15); dorsal- and anal-fin rays all unbranched, all segmented except

anteriormost one and posteriormost one or two soft rays; pectoral fin 19 (17–20, 18); pelvic fin, if present, I,3 (I,3), rays unsegmented in primary male, second and third ray segmented in secondary male; upper and lower segmented caudal-fin rays 8+7 (7–8+6–7, 8+7); upper and lower branched caudal-fin rays 6+5 (6+5–6, 6+5); procurent caudal rays in paratypes vii–x (ix; upper), viii–x (ix=x; lower); P–V 10 (10 or 9–10, 10); vertebrae 10+15=25 (10+15=25); scales totally absent.

Body strongly compressed and elongate. Eyes lateral. Mouth terminal to supraterminal, inclined obliquely upwards. First dorsal fin absent. Origin of second dorsal fin slightly posterior to vertical line through anus. Origin of anal fin beneath base of second ray of dorsal fin. Caudal fin slightly emarginate. Pectoral fin rounded. All rays except for some of caudal fin unbranched.

Sensory papillae on head in transverse pattern, some present on branchiostegal region (Figs. 6–8).

Maxillo-vomerine meniscus present. In secondary male, ectopterygoid and quadrate widely separated by unossified connective tissue. Pelvis a long rod. Left and right pelvic bones separated from each other posteriorly. Subpelvic process absent. Posteriormost dorsal- and anal-fin pterygiophore each supporting one unbranched soft ray.

Etymology. The generic name *Paedogobius* refers to the goby having a larval-like (paedomorphic) body.

New common name: *Shirasukiba-haze-zoku* (Japanese).

Paedogobius kimurai n.sp.

Figs. 1–8, Table 1

Goby L—Miskiewicz, 1987: 113–116, 145, 147, figs. 4.33, 5.58, table 4.45.

Gobiid sp. 1 (wide-gape paedomorphic goby)—Neira & Miskiewicz, 1998: 394–395, fig. 121a–f.

Type material. HOLOTYPE: NSMT-P52628, secondary ♂, 14.8 mm (standard length), Amitori Bay (24°19'N 123°42'E), Iriomote Island, Taketomi cho, Yaeyama gun, Okinawa Prefecture, Japan, 30 October 1994. PARATYPES: AMS I.37857-001, secondary ♂, 14.2, collection locality as for holotype, 31 October 1995; BLIH 1994022, secondary ♂, 14.8, same data as previous; FAKU 65770, secondary ♂, 14.1, same data as previous; NTM S.14628-001, secondary ♂, 14.2, same data as previous; USNM 344538, secondary ♂, 14.1, same data as previous; NTM S.14596-001, secondary ♂, 15.4, collection locality as for holotype, 10 July 1996; AMS I.37858-001, ♀, 15.2, Nakagusuku Bay (26°12'N 127°50'E), Okinawa Island, Okinawa Prefecture, Japan, 29 May 1994; BLIH 1994025, ♀, 15.5, same data as previous; BLIH 1994026, secondary ♂, 16.1, same data as previous; BMNH 1997.4.22:3, ♀, 15.7, same data as previous; NSMT-P52631, ♀, 15.3, same data as previous; USNM 344539, ♀, 14.3, same data as previous; YCM-P33070, secondary ♂, 16.4, same data as previous; YCM-P33072, ♀, 16.2, same data as previous;

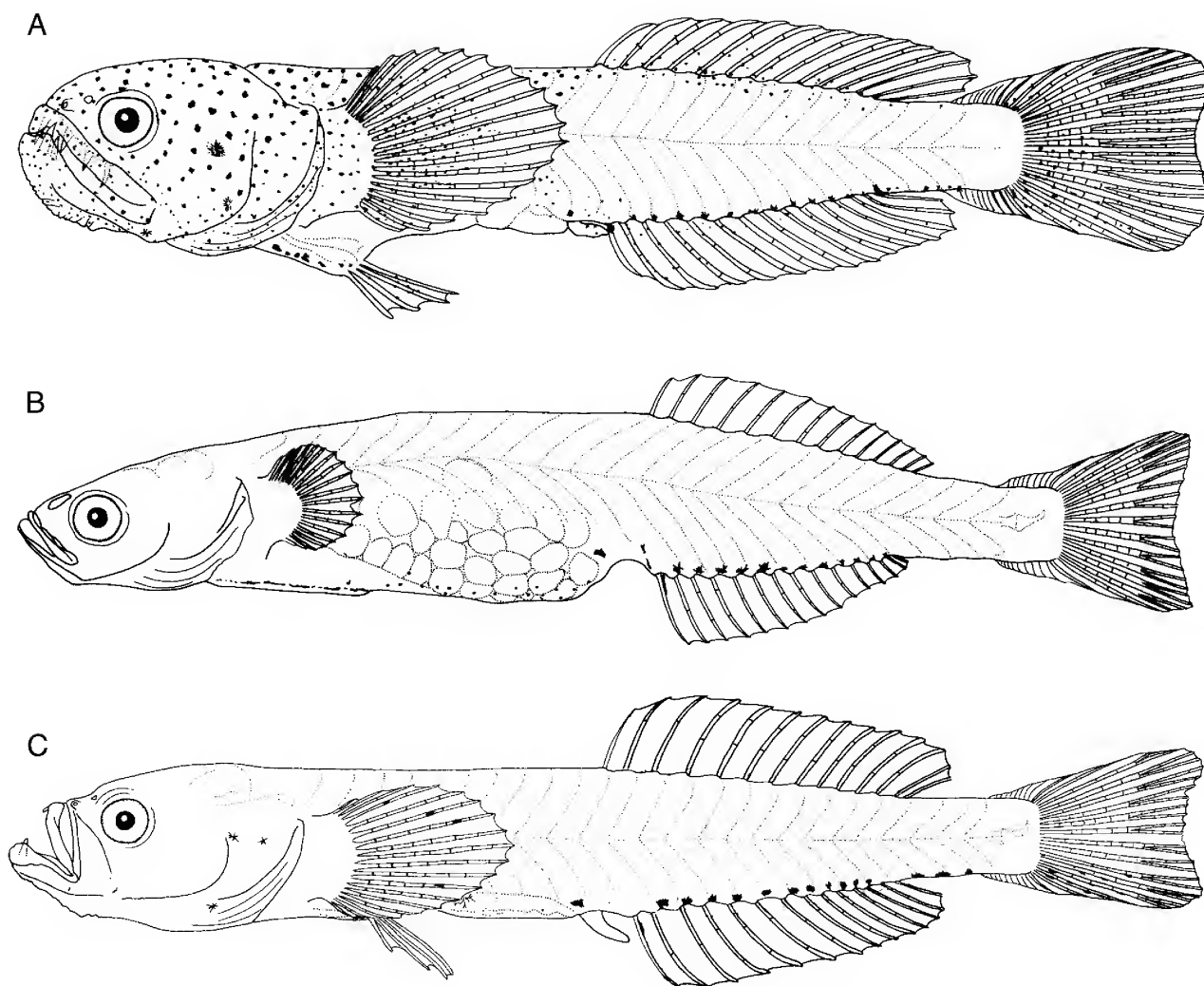


Figure 1. *Paedogobius kimurai* n.gen. and n.sp. A, holotype, NSMT-P52628, secondary ♂, 14.8 mm SL; B, paratype, NSMT-P52630, ♀, 15.2 mm SL, note ovarian eggs visible through body wall; C, paratype, NSMT-P52629, primary ♂, 12.0 mm SL.

ZUMT 59947, secondary ♂, 16.9, same data as previous; FAKU 65771, ♀, 15.8, collection locality as for AMS I.37858-001, 13 May 1994; YCM-P33071, ♀, 14.8, same data as previous; ZUMT 59948, ♀, 15.7, same data as previous; BMNH 1997.4.22:2, secondary ♂, 14.9, collection locality as for AMS I.37858-001, 30 May 1994; AMS I.37859-001, ♀, 14.7, collection locality as for AMS I.37858-001, 8 June 1994; BLIH 1994023, primary ♂, 11.3, same data as previous; BLIH 1994024, ♀, 15.5, same data as previous; BMNH 1997.4.22:4, ♀, 14.7, same data as previous; FAKU 65769, primary ♂, 12.0, same data as previous; FAKU 65772, ♀, 15.4, same data as previous; NSMT-P52629, primary ♂, 12.0, same data as previous; NSMT-P52630, ♀, 15.2, same data as previous; USNM 344540, ♀, 14.7, same data as previous; ZUMT 59949, ♀, 14.7, same data as previous; ZUMT 59950, primary ♂, 11.8, same data as previous; NTM S.14595-001, ♀, 14.4, collection locality as for AMS I.37858-001, 9 June 1994; NTM S.14595-002, ♀, 14.1, same data as previous.

Non-type material. SIO 61-655, 5 (1 ♀ and 4 secondary ♂ ♂), 11.2, 11.8–13.5, Gulf of Thailand (12°18.5'N 101°05.2'E), Thailand, 20 March 1960, Naga Expedition; AMS I.33290-005, 3 (all ♀ ♀), 10.2, 9.9 and 9.6, inshore of Pandora Reef, Queensland (18°49'S 146°26'E), Australia, 17–20 March 1983, collected by D. Williams; AMS I.33290-006, 2 (1 secondary ♂ and 1 ♀ or primary ♂), 10.7, 10.1, collection locality and date as for AMS I.33290-005; BLIH 1985501, ♀, 12.9, Hanejinaikai Bay (26°39'N 128°01'E), Okinawa Island, Okinawa Prefecture, Japan, 17 October 1985; BLIH 1985502, ♀, 12.6, same data as previous; BLIH 1986704, ♀, 6.9, same collection locality as previous, 20 November 1986; BLIH 1988350, ♀, 11.2, Itoman Bay (26°07'N 127°39'E), Okinawa Island, Okinawa Prefecture, Japan, 3 June 1988; BLIH 1988351, ♀, 16.5, same collection locality as previous, 30 December 1988; BLIH 1989239, ♀, 9.2, same collection locality as previous, 10 September 1989; BLIH 1989240, secondary ♂, 14.6, same data as previous.

Table 1. Proportional measurements in percent of standard length of *Paedogobius kimurai* n.gen. and n.sp.

	secondary males holotype N = 1	paratypes N = 8	primary males paratypes N = 4	females paratypes N = 18
total length	118.2	115.5–120.6	115.0–121.2	112.5–118.4
head length	31.1	29.9–33.8	26.5–29.2	22.7–25.2
head depth at preopercular margin	20.9	19.6–21.4	15.3–16.7	13.8–15.6
body depth at pelvic-fin base	23.0	18.9–23.6	15.8–18.3	15.1–18.4
body depth at anal-fin origin	16.9	14.9–16.6	15.0–16.1	15.0–17.0
preanal length	53.4	52.4–55.4	52.2–55.0	55.1–62.4
snout length	7.4	6.8–8.5	5.9–7.5	5.2–6.8
head width at preopercular margin	20.9	13.4–20.3	12.4–14.2	10.2–12.6
body width at pectoral-fin base	12.2	10.1–12.8	8.8–10.2	6.8–9.7
body width at anal-fin origin	6.1	5.9–7.1	4.4–5.9	5.0–6.5
maxillary length	18.2	15.9–19.1	9.3–10.6	5.2–9.8
eye diameter	6.1	4.7–6.5	4.4–5.1	4.4–5.7
interorbital width	8.8	8.8–11.3	6.8–9.2	4.8–7.8
caudal peduncle length	14.2	13.5–16.5	13.6–18.3	13.4–17.0
caudal peduncle depth	9.5	8.5–9.2	7.5–8.5	7.0–8.3
longest pelvic-fin ray	9.5	7.9–10.7	6.8–11.7	absent
longest pectoral-fin ray	17.6	15.5–17.6	13.6–18.6	6.6–8.5
second dorsal-fin base	30.4	25.4–29.0	28.8–29.2	24.7–29.7
anal-fin base	27.4	23.9–28.4	26.3–27.4	22.8–28.4
snout to second dorsal-fin origin	54.7	56.7–59.2	55.9–58.4	57.6–63.2
snout to second dorsal-fin end	83.8	83.8–86.5	83.9–86.7	82.3–87.8
snout to anal-fin origin	56.8	57.3–60.6	54.9–61.7	57.8–62.1
snout to anal-fin end	81.8	82.5–85.8	82.3–85.8	82.9–87.8

Cleared and stained specimens (non type material). BLIH 1994032, primary ♂, 11.7, BLIH 1994042, primary ♂, 12.2, these with collection locality and date as for AMS I.37859-001; BLIH 1994033 ♀ 15.2, BLIH 1994034 secondary ♂ 16.6, BLIH 1994035 secondary ♂ 16.3, BLIH 1994036 ♀ 16.3, BLIH 1994037 ♀ 15.5, BLIH 1994038 ♀ 14.3, these with collection locality and date as for AMS I.37858-001; BLIH 1994039 secondary ♂ 15.9, BLIH 1994040 secondary ♂ 14.5, BLIH 1994041 ♀ 14.1, these with collection locality and date as for BMNH 1997.4.22:2; BLIH 1995033, secondary ♂, 14.8, collection locality as for holotype, 30 October 1995; BLIH 1995034, secondary ♂, 14.8, same data as previous; BLIH 1989238, ♀, 6.6, collection locality and date as for BLIH 1989239.

Diagnosis. See generic diagnosis.

Description. *Counts*—See generic description. *Measurements*—data for range of paratypes (except BLIH 1994026 and BMNH 1997.4.22:2) given first, followed by holotype data in parentheses.

Female. Body depth at pelvic-fin base 5.4–6.6 in SL, body depth at anal-fin origin 5.9–6.7 in SL, body width at pectoral-fin base 10.3–14.7 in SL, body width at anal-fin

origin 15.5–20.1 in SL, head length 4.0–4.4 in SL, head width at preopercular margin 1.2–1.5 in head depth at preopercular margin, snout length 3.7–4.8 in head length, eye diameter 4.5–5.3 in head length.

Primary male. Body depth at pelvic-fin base 5.5–6.3 in SL, body depth at anal-fin origin 6.2–6.7 in SL, body width at pectoral-fin base 9.8–11.3 in SL, body width at anal-fin origin 16.9–22.6 in SL, head length 3.4–3.8 in SL, head width at preopercular margin 1.2–1.3 in head depth at preopercular margin, snout length 3.9–4.3 in head length, eye diameter 5.3–6.0 in head length.

Secondary male. Body depth at pelvic-fin base 4.2–5.3 (4.4) in SL, body depth at anal-fin origin 6.0–6.7 (5.9) in SL, body width at pectoral-fin base 7.8–9.9 (8.2) in SL, body width at anal-fin origin 14.1–16.9 (16.4) in SL, head length 3.0–3.3 (3.2) in SL, head width at preopercular margin 1.0–1.5 (1.0) in head depth at preopercular margin, snout length 3.8–4.5 (4.2) in head length, eye diameter 5.0–6.4 (5.1) in head length.

Head and body shape. Female. Head strongly compressed. Nostril a single shallow pit. Dorsal profile from nape to origin of dorsal fin slightly convex. Maxilla extends to

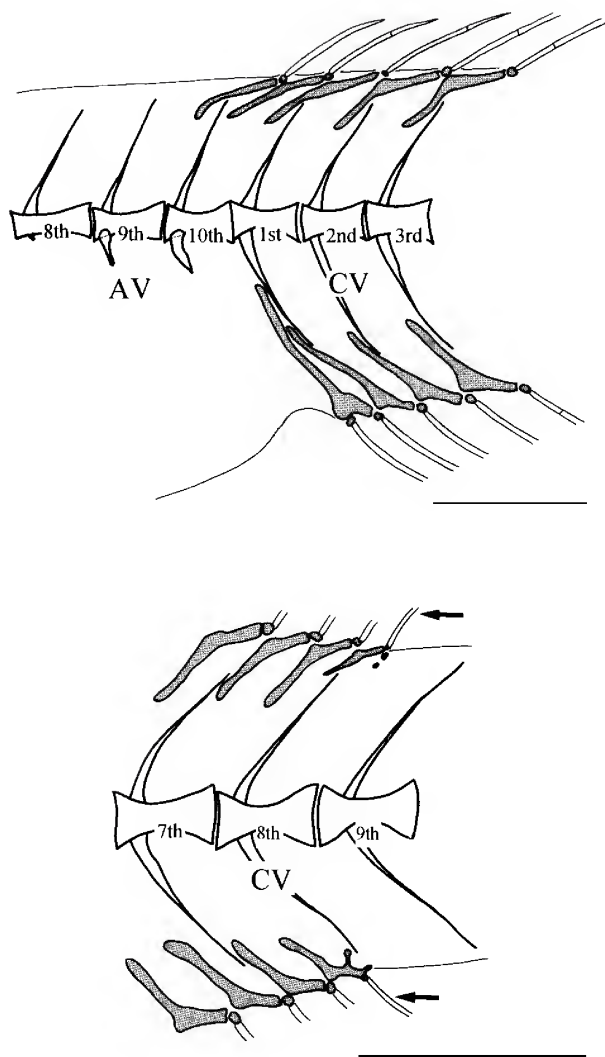
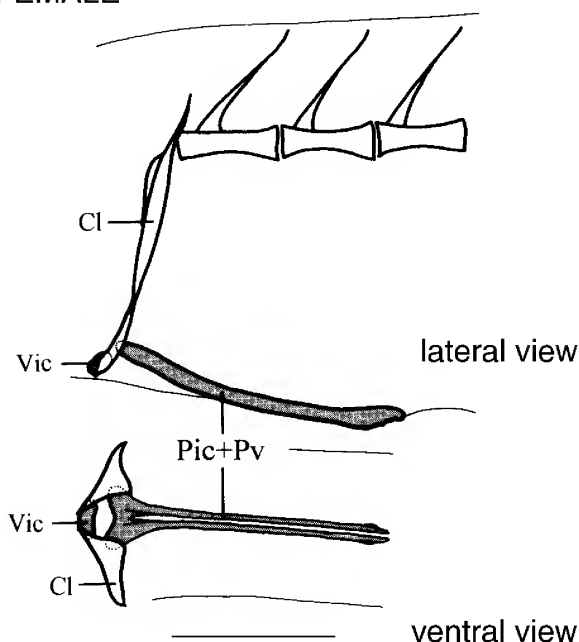


Figure 2. Vertebrae, and anterior and posterior parts of dorsal- and anal-fin of *Paedogobius kimurai* (♀, BLIH 1994033). Abbreviations: AV, abdominal vertebrae; CV, caudal vertebrae. Arrows indicate unbranched last dorsal and anal soft rays. Scale bars are 1 mm. Shading = cartilage or unossified bone.

below front of eye. Lower jaw prominent. Upper and lower jaw with series of small conical teeth. Anteroventral margin of gill opening reaching to point below posterior end of pupil, lower end of branchiostegal membranes attaching at middle point of isthmus. Urogenital papilla absent. Pectoral fin small, posterior tip slightly anterior to vertical line through posterior end of pelvis. Pelvic fin absent. Posterior ends of dorsal and anal fins widely separated from upper and lower origin of caudal fin. Upper and lower ends of caudal fin weakly pointed. Ovary visible in abdomen through transparent body. Upper half of quadrate and pelvis unossified.

Primary male. Head strongly compressed. Two nostrils present, anterior with short tube. Dorsal profile, from nape to origin of dorsal fin, almost straight. Maxilla extends to

FEMALE



SECONDARY MALE

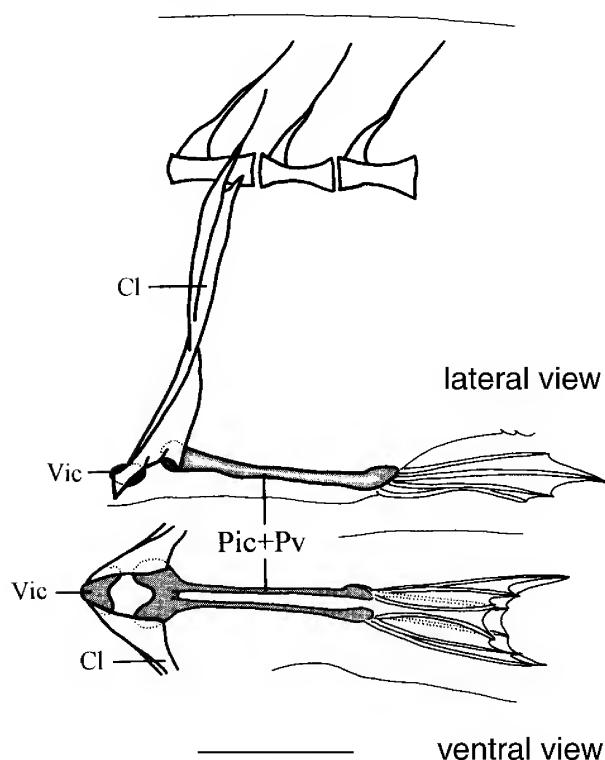
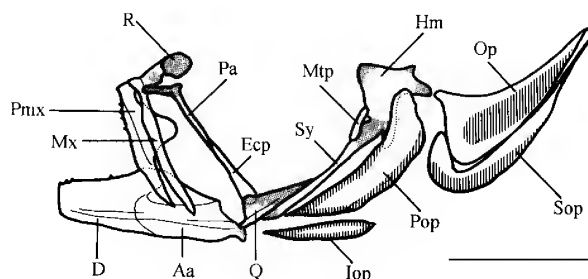
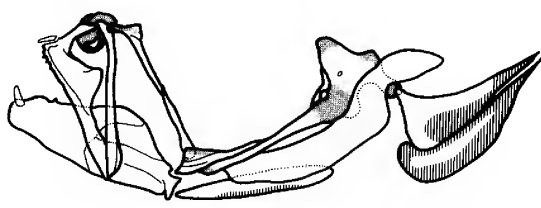


Figure 3. Lateral and ventral view of left pectoral and pelvic girdles of *Paedogobius kimurai* (♀, BLIH 1994033; secondary ♂, BLIH 1994034). Abbreviations: Cl, cleithrum; Pic+Pv, pelvic intercleithral cartilage and pelvis; Vic, ventral intercleithral cartilage. Scale bars are 1 mm.

FEMALE



PRIMARY MALE



SECONDARY MALE

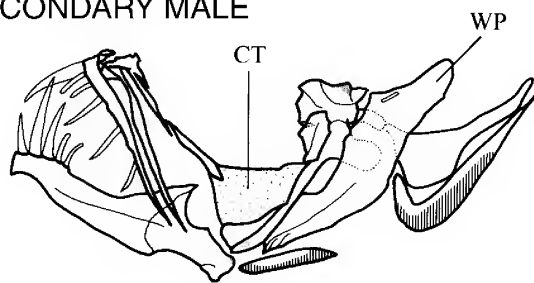
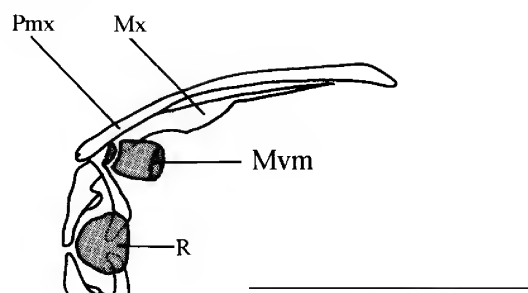


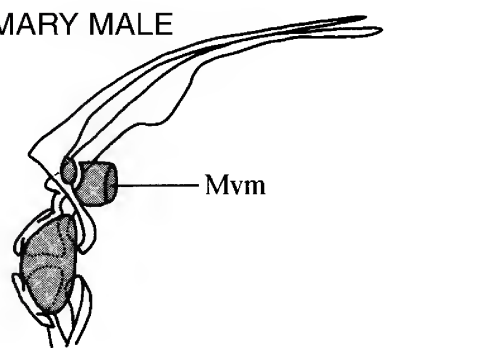
Figure 4. Left lateral view of jaws and suspensorium of *Paedogobius kimurai* (♀, BLIH 1994033; primary ♂, BLIH 1994032; secondary ♂, BLIH 1994034). Abbreviations: Aa, anguloarticular; CT, connecting tissue; D, dentary; Ecp, ectopterygoid; Hm, hyomandibula; Iop, interopercle; Mtp, metapterygoid; Mx, maxilla; Op, opercle; Pa, palatine; Pmx, premaxilla; Pop, preopercle; Q, quadrate; R, rostral; Sop, subopercle; Sy, symplectic; WP, wing-like projection of preoperculum. Ossified rostral of secondary ♂ hidden by maxilla and premaxilla. Scale bars are 1 mm. Shading = cartilage; stippling = connective tissue; striping = decalcified area.

below front part of eye. Five and two conical teeth across front of upper and lower jaws respectively, anteriormost tooth of both jaws largest. Anteroventral margin of gill opening reaches point below anterior end of pupil, lower end of branchiostegal membranes attach at middle point of isthmus. A slender urogenital papilla present, curving backward. Pectoral fin of moderate size, posterior tip reaches to vertical line through mid point between origins of pelvic and anal fins. Pelvic fin present with complete

FEMALE



PRIMARY MALE



SECONDARY MALE

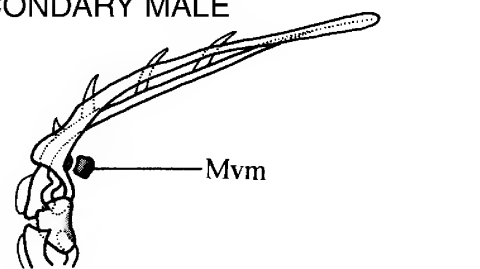


Figure 5. Dorsal view of rostral and right upper jaws of *Paedogobius kimurai* (♀, BLIH 1994033; primary ♂, BLIH 1994032; secondary ♂, BLIH 1994034). Abbreviations: Mvm, maxillo-vomerine meniscus; Mx, maxilla; Pmx, premaxilla; R, rostral. Scale bars are 1 mm. Shading = cartilage.

frenum and connecting membrane between third rays, forming long disc; when appressed, posterior end reaches midpoint between origin of pelvic fin and anus. Posterior ends of dorsal and anal fins widely separated from upper and lower origin of caudal fin. Upper and lower margins of caudal fin weakly rounded. Cartilaginous area on anterior part of quadrate narrow. Posterior two-thirds of pelvis weakly ossified laterally.

Secondary male. Head large, rounded, slightly compressed, temporal region may be inflated. Two nostrils present, anterior with short tube. Dorsal profile, from nape to origin of dorsal fin, almost straight. Anterior margin of upper jaw with concavity on each side, behind jaw tip, and anterior margin of lower jaw with convexity on each side. Maxilla extends beyond rear of eye. Upper jaw with single series of six large canine-like teeth on each side, anteriormost largest, second and third smaller, with blunt tips. Lower jaw with series of five large canine-like teeth on each side, concentrated on anterior part of jaw, second largest, fourth and fifth have blunt tip, one tooth with blunt tip present just behind anteriormost tooth (hidden by second large tooth in Fig. 4). Anteroventral margin of gill opening reaches to point below halfway between posterior end of eye and preopercle, lower end of branchiostegal membranes attaches at middle point of isthmus. A slender, elongate urogenital papilla present, curving backward. Pectoral fin large, posterior end reaches to vertical line through anus. Pelvic fin present with complete frenum and connecting membrane between third rays, forming long disc, posterior end reaches to mid-point between origin of pelvic fin and anus. Posterior ends of dorsal and anal fins widely separated from upper and lower origin of caudal fin. Upper and lower margins of caudal fin rounded. Rostral cartilage and quadrate ossified (Fig. 5). Pelvis weakly ossified laterally. A large wing-like projection present on upper posterior end of preopercle.

Cephalic lateral line system. Description of cephalic lateral line system based on the following specimens: ♀, BLIH 1994024; primary ♂, BLIH 1994023; secondary ♂, BLIH 1994026.

Female. Sensory canal and canal pore absent. Two longitudinal papillae rows on dorsal surface of snout. A broken transverse papillae row across interorbital. A long transverse papillae row across anterior occiput. Two short, longitudinal papillae rows on posterior occiput. Two short, transverse papillae rows on dorsolateral side of posterior occiput. Two longitudinal and one transverse papillae rows on side of snout anterior to eye. Three transverse papillae rows on cheek below eye. Two short, longitudinal papillae rows containing two papillae directly behind eye. A pair of longitudinal papillae rows on chin. Two papillae on branchiostegal region. One to several papillae around nostril, on both sides of interorbital, cheek, operculum, and along lower edge of preopercle and lower jaw, sometimes forming short rows.

Primary male. Sensory canal and canal pore absent. Two or three pairs of longitudinal papillae rows on dorsal surface of snout. A long transverse papillae row across interorbital. A long, transverse papillae row across anterior occiput. Two short, transverse papillae rows on dorsolateral side of anterior occiput. Two longitudinal papillae rows on posterior occiput. Two short, transverse papillae rows on dorsolateral side of posterior occiput. Longitudinal, diagonal and transverse papillae rows on side of snout anterior to eye. Five transverse diagonal papillae rows on cheek below and behind of eye. Two longitudinal papillae rows on chin. Three

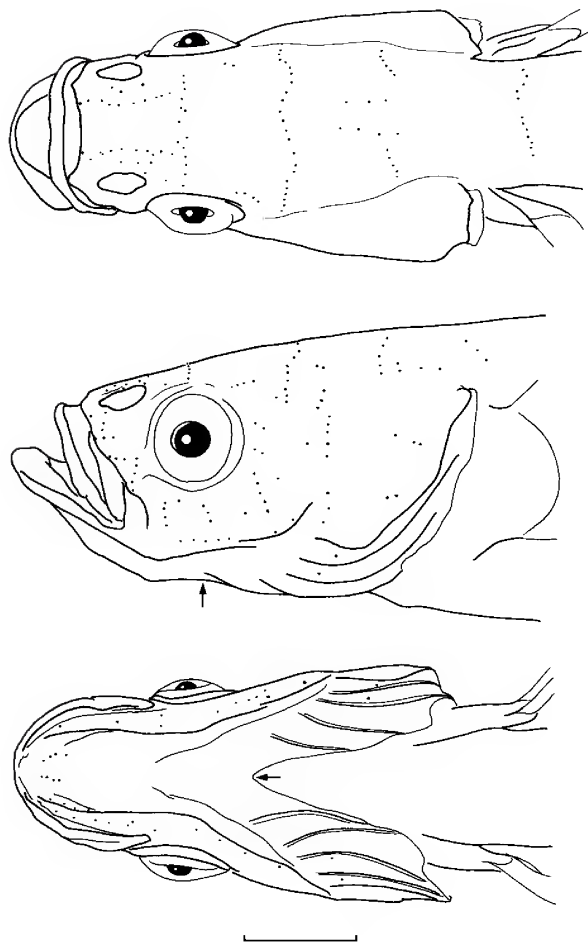


Figure 6. Cephalic lateral line system of dorsal, lateral, and ventral side of female of *Paedogobius kimurai*, BLIH 1994024 (15.5 mm SL). Dots represent the sensory papillae; and the arrow points to where the gill membranes attach to the isthmus. Scale bar 1 mm.

papillae on branchiostegal region. One to several papillae around nostrils, on each side of interorbital, nape, cheek, operculum, and along lower edge of preopercle and lower jaw, sometimes forming short rows.

Secondary male. Sensory canal and canal pore absent. Two longitudinal papillae rows on dorsal surface of snout with two transverse rows between them. A broken transverse papillae row on interorbital. A long, transverse papillae row across anterior occiput. Two short, transverse papillae rows on dorsolateral side of anterior occiput. Two longitudinal papillae rows on posterior occiput. Two short, transverse papillae rows on dorsolateral side of posterior occiput. Three diagonal or transverse papillae rows on side of snout anterior to eye. Five transverse or diagonal papillae rows on cheek below and behind eye. Two longitudinal papillae rows on chin. Three papillae on branchiostegal region. One to several papillae around nostrils, on each side of interorbital, nape, cheek, operculum, and along lower edge of preopercle and lower jaw, sometimes forming short rows.

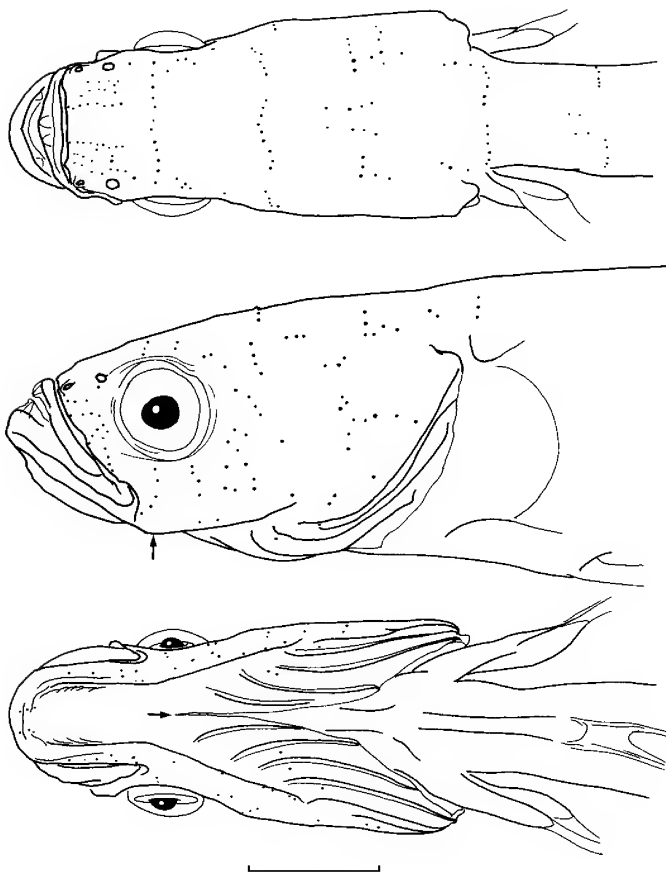


Figure 7. Cephalic lateral line system of dorsal, lateral, and ventral side of primary male of *Paedogobius kimurai*, BLIH 1994023 (11.3 mm SL). Dots represent the sensory papillae; and the arrow points to where the gill membranes attach to the isthmus. Scale bar is 1 mm.

Coloration. Female. A row of melanophores along anal-fin base, also on ventral midline of lower edge of caudal peduncle in some individuals. An elongate melanophore along upper rear edge of first anal-fin ray. Single melanophore on inner side of upper part of anus; one or two melanophores on inner side of posterodorsal part of anus in some individuals. Many small granule-like melanophores on ventral surface of abdomen. A row of melanophores on inner side of pelvis. Several melanophores on lower half of caudal-fin rays, near base, in some individuals. Peritoneum unpigmented. Anterodorsal portion of swim-bladder pigmented, with dendritic melanophores.

Primary male. A row of melanophores on anal-fin base and ventral midline of lower edge of caudal peduncle. An elongate melanophore along upper rear edge of first anal ray. A melanophore on inner side of upper part of anus. Two dendritic melanophores on testis (one hidden by pectoral fin in Fig. 1). A row of melanophores on inner side of pelvis. Several melanophores on lower half of caudal-fin rays, near base. Several melanophores on some pectoral-fin rays. Two small dendritic melanophores on operculum, and one on branchiostegal region. Peritoneum unpigmented.

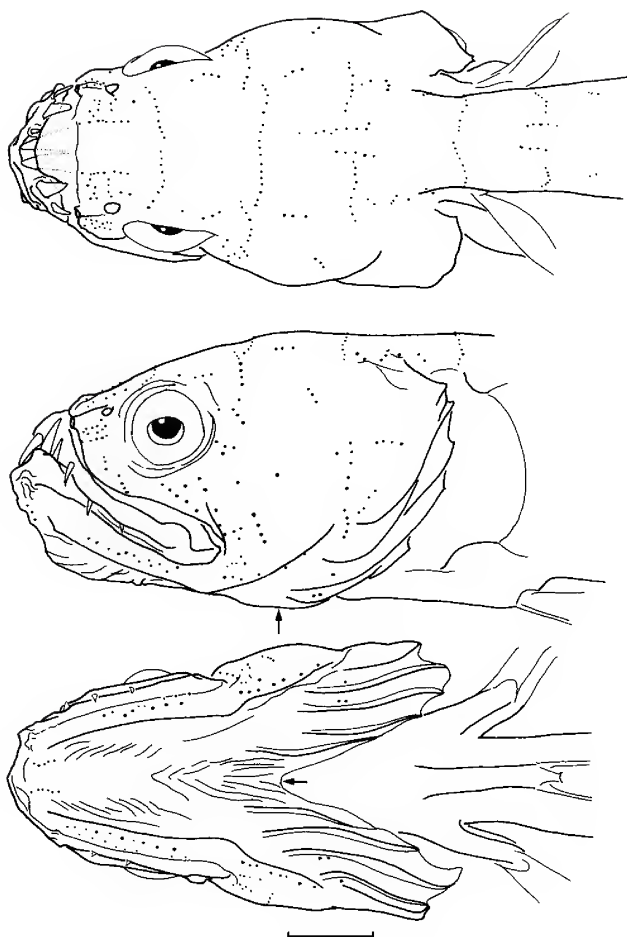


Figure 8. Cephalic lateral line system of dorsal, lateral, and ventral side of secondary male of *Paedogobius kimurai*, BLIH 1994026 (16.1 mm SL). Dots represent the sensory papillae; and the arrow points to where the gill membranes attach to the isthmus. Scale bar is 1 mm.

Anterodorsal portion of swim-bladder pigmented, with dendritic melanophores.

Secondary male. A row of melanophores on anal-fin base and ventral midline of lower edge of caudal peduncle. Many melanophores on caudal-fin rays near base, on lower half of dorsal and anal fins, on anterior half of pectoral fin and posterior part of pelvic fin. Some melanophores on urogenital papilla. Many melanophores on body, with largest on the anterior half, especially on head. Peritoneum unpigmented. Anterodorsal portion of swim-bladder pigmented, with dendritic melanophores.

Distribution. AUSTRALIA (New South Wales and Queensland), Botany Bay (34°00'S 151°11'E), Hawkesbury River (33°30'S 151°10'E), Lake Macquarie (33°05'S 151°35'E), Pandora Reef (18°49'S 146°26'E) (after Neira & Miskiewicz, 1998); THAILAND, Gulf of Thailand (12°18.5'N 101°05.2'E); JAPAN, Hanejinaikai Bay (26°39'N 128°01'E), Itoman Bay (26°07'N 127°39'E) and Nakagusuku Bay (26°12'N 127°50'E) at Okinawa Island, Amitori Bay (24°19'N 123°42'E) at Iriomote Island.

Etymology. The specific epithet, *kimurai*, is for Mr Motofumi Kimura, who first discovered this species in Japan.

Common names: Wide-gape paedomorphic goby (English) or *Shirasukiba-haze* (Japanese).

Discussion

The differences in head and body shapes between the female and secondary male *Paedogobius* are striking. However, unquestionable evidence as to the species' identification exists; under aquarium conditions, females, about one week after spawning, undergo a change in form to become secondary males. The females reared in captivity were collected in Nakagusuku Bay using *Shirasu*-Patch net, a kind of specialised net used in a fishery for juvenile sardines. All fishes collected by this net died, apart from those individuals used in the aquarium experiment, which were got to the laboratory quickly by sorting on them on-board. No male was present among the captive fish used in the experiment. The females were fed live *Artemia* and spawned in the aquarium two or three days after collection. A mass of 27 eggs was studied. The eggs formed a single mass, tangled together by a series of filaments arising from the basal part of each egg. The eggs were long and ellipsoid, 2.6–2.8 mm and 0.5 mm in long and short axes, respectively. These eggs did not develop because they were not fertilized.

The second author continued rearing the same captive females in the same aquarium. The females changed head and body shape, pelvic fins developed gradually, and the fish developed into secondary males about one week after spawning. Accordingly, it is apparent that the females changed sex after spawning. In addition, the changing process (accompanying maturity from immature male to primary male), as well as the sex change from female to secondary male, was observed in many specimens collected from Nakagusuku Bay, Okinawa Island, Japan. Both primary and secondary males possess ripe sperm (Dr A. Hattori, pers. comm.).

Paedogobius kimurai differs from all known genera of Gobiidae in having a characteristic pelvis shape, and a unique widely separated ectopterygoid and quadrate in the secondary male. Additionally, there has been no previous verified report of sex-change in the broad group to which *Paedogobius* belongs, the Gobionellinae (Dr Kassi Cole, pers. comm.).

Johnson & Brothers (1993) included *Schindleria* in the Gobioidaei. *Paedogobius* shares some characters with *Schindleria*, including a maxillo-vomerine meniscus, one unbranched ray supported by the last pterygiophore of the dorsal and anal fin, and a transparent body. However, it differs from the latter in a number of ways, such as having a pelvis, a urostyle similar to second preural centrum in length, fewer vertebrae, and in the deeper body.

Paedogobius belongs in the *Gobiopterus* group *sensu* Birdsong *et al.* (1988) (*Brachygobius*, *Gobiopterus*, *Mistichthys*, *Pandaka*) in having a 10+15 vertebral count and a similar geographic distribution. The general appearance of male *Gobiopterus* bears some resemblance to the secondary males of *Paedogobius*, in having a rounded robust head, large canine-like teeth in both jaws and

transverse sensory papillae. Larson (in press) discusses the relationships of this group, stating that *Brachygobius* and *Pandaka* are sister-taxa (and are related to *Stigmatogobius* and *Mugilogobius*). *Gobiopterus* and *Mistichthys* share several characters with *Brachygobius* and *Pandaka*: all segmented rays in second dorsal and anal fins, 10+15 vertebrae, two anal-fin pterygiophores inserting before the first caudal vertebra, and one or two, usually two, epurals. *Brachygobius* and *Pandaka* differ from the transparent larval-like *Gobiopterus* and *Mistichthys* in their conspicuous banded or spotted black and white colour patterns.

Paedogobius bears some resemblance (especially secondary males) to *Gobiopterus* and *Mistichthys*, which are also dwarf, paedomorphic gobiids. Neither genus has been reviewed or clearly diagnosed in the literature, but these taxa are presently being revised by the third author. Some preliminary diagnostic information is provided here, based on observations of eight species of *Gobiopterus* and the single nominal species of *Mistichthys* (opinions of third author).

Mistichthys is considered as monotypic (*M. luzonensis* Smith), known only from Lake Buhi, Luzon, in the Philippines. There is little sexual dimorphism in adult size and none in tooth form: both sexes have a single row of small, fine, pointed teeth in each jaw; there are II–IV first dorsal-fin rays, the gill opening is wide and may reach to posterior edge of eye; scales are present on the body, and the jaws are terminal, oblique, but not nearly vertical.

Gobiopterus includes about 14 nominal species, all of which appear to be sexually dimorphic (males and females have been described as separate species), known from brackish lakes, estuaries and mangroves in the Indo-West Pacific. *Gobiopterus* males may be larger than females and have enlarged, flattened, caniniform teeth (teeth small, sharp and evenly sized in females). These fish have III–V (usually V) first dorsal-fin spines, the gill opening is variable, from below the opercle to halfway between preopercular margin and the posterior edge of the eye; the jaws are strongly oblique to nearly vertical in large males; and scales are usually present.

Paedogobius differs from these two genera in lacking a first dorsal fin (present in *Gobiopterus* and *Mistichthys*), having 1,3 pelvic-fin rays (1,5 in *Gobiopterus* and *Mistichthys*), a greater number of fin rays (13–16 second dorsal-fin rays versus 7–9 in *Gobiopterus* and *Mistichthys*), a wide gill opening which varies from under mid-eye in female and primary male and under preopercle in secondary male (gill opening to at least rear margin of eye in *Mistichthys* and under opercle or preopercle in *Gobiopterus*), lacking scales (scale cover present in varying degrees in *Gobiopterus* and *Mistichthys*), and different pelvis form.

The rod-like pelvis shape in *Paedogobius* is similar to that of *Gobiopterus* and its relative *Mistichthys*. The pelvis in these genera, however, differs from that of *Paedogobius* in the following characters: pelvis shorter, not extending past vertical line through posterior end of second abdominal vertebra in *Gobiopterus*, may just reach past posterior end of second vertebra in *Mistichthys* (vs extending to vertical line through mid point of third abdominal vertebra in

Paedogobius); subpelvic process present in males (vs absent in both sexes) and posterior ends of left and right pelvic bones almost attached or attached to each other (vs posterior ends always clearly separated from each other).

Separation of the ectopterygoid and quadrate is unusual among gobiids, being found only in the secondary male of this genus. Also, the secondary male can open its mouth a full 180°. The separation of ectopterygoid and quadrate makes this possible, along with the strong adductor mandibulae muscles which attach posteriorly to a large, wing-like dorsal projection of the preopercle (Figs. 4 and 9). Although their wide jaws and teeth resemble that of secondary male *Paedogobius*, large adult male *Gobiopterus* possess a preopercle resembling that of a female *Paedogobius* and the jaws cannot be gaped so widely.

Miskiewicz (1987) and Neira & Miskiewicz (1998) describe and illustrate the larval stages of this species. The pigment along the ventral mid-line of the caudal peduncle and the teeth form early in development.

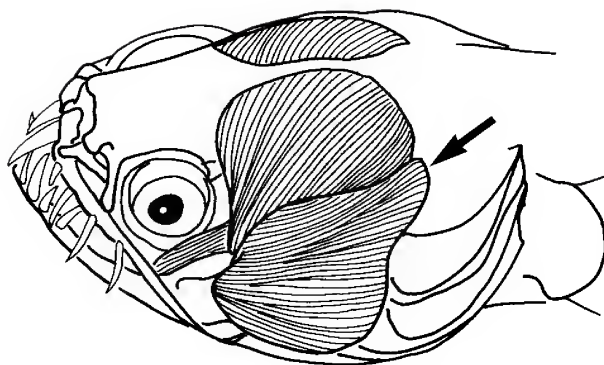


Figure 9. Adductor mandibulae muscles in BLIH 1995033 (14.8 mm SL). Arrow points to posterior attachment on wing-like projection of preoperculum.

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